### THE FOSSIL HISTORY OF THE EMUS, DROMAIUS (AVES: DROMAIINAE)

# C. PATTERSON & P. V. RICH

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The oldest known emu is Dromaus gidju n. sp. from the medial Miocene Kutjamarpu fauna at Lake Ngapakaldi in northern South Australia This form, based on a partial hind limb, is smaller and has relatively shorter and less mediolaterally compressed hind limb bones, and less reduction of the medial and lateral digits than in the living form. D. gidju thus appears to be less specialized for a cursorial lifestyle, being somewhat intermediate between the forest dwelling cassowaries and the highly cursorial living enu, D. novaehollandiae, Fossils from the Late Miocene and Early Pliocene may be allied to D. gidju, but more material is needed to allow confident assignment. D. ocypus from the medial Pliocene Palankarinna fauna at Lake Palankarinna, northern South Australia, is imermediate in size between D. gidju and D. novaehollandiae. In addition, its tarsometatarsus is decidedly shorter relative to width than that in D novaehollandiae, thus indicating that it is not as highly adapted for a cursorial life as the living emu. Essentially all other emu fossils, Late Phocene-Recent, appear to belong in D. novaehollandiae including: D. 'putricius', D. 'gracilipes', and 'Metapteryx bifrons', all defined originally by C.W. De Vis. The only exceptions are the King Island emu (D. ater) and the Kangaroo Island cmu (D. baudiniumus). Whether there was greater size variability in Pleistocene emu populations and whether a separate species of entu once inhabited Tasmania are problems yet to be resolved once larger collections of both living and fossil emus can be measured and analyzed.

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The living enu (Dromaius novaehollandiae) is the second largest living ground bird, exceeded only by the ostrich in size. Today and in the past, emus have been restricted to Australia, and their origins are not understood.

The fossil record of emus begins in the Miocene, with two now extinct species occurring one each in the Pliocene and the Miocene of northern South Australia. The Quaternary King Island and Kangaroo Island emus seem to belong in two separate species. All other fossil emus, mainly Pleistocene, however, are very similar to and most probably conspective with the living *D. novaehollandiae*. It is very likely, however, that the history of emus on the Australian continent is much older than currently understood because of the general lack of a pre-Miocene terrestrial record.

Although the Pleistocene emus are currently indistinguishable from the living emu, the Tertiary species are distinct. The hind limb of the single Miocene form is not as cursoitally adapted. This species has a tarsometatarsus that is shorter and more robust, and the lateral and medial digits of the foot are not as reduced as in the living emu.

This paper reviews fossil emu material and outlines the major evolutionary trends demonstrated by the dromaiines during the last 20 million years.

The following abbreviations are used:

- AM Australian Museum, Sydney
- AMNH American Museum of Natural History, New York

B.P.	Years before present
<i>C</i> .	Cranium, crania
Cor.	Coracoid
CSIRO	Commonwealth Scientific and
	Industrial Research Organization,
	Division of Wildlite and Rangelands
	Research, Canberra
d	Distal
diapop.	Diapophyses
est.	Estimated
E	Femur
Fib,	Fibula
HM	Hunterian Museum, Glasgow
hum.	Humerus ·
juv	Juvenile
L	Left
M	Mandible
MM	Geological and Mining Museum,
	Sydney
NMV	Museum of Victoria, Melbourne
р	Proximal
Ph.	Phalanx, phalanges
postzyg.	Postzygapophyses
QM	Queensland Museum, Brisbanc
QVM	Queen Victoria Museum and Art
	Gallery, Launceston
R(r)	Right
SAM	South Australian Museum, Adelaide
SIAM	Smithsonian Institution - American
	Museum of Natural History
	Expedition Field Numbers,
	Washington, D.C. and New York
Sk.	Skeleton(s), many skeletal elements
Sr.	Sternum
Syn.	Synsacrum

T2, T3, T	4 Trochleae II, III, IV
Tih	Tibiotarsus-
Tru	Tarsometatarsus
K	Veriebra(c)
UCMP	University of California, Museum of Paleontology, Berkeley
WAM	Western Australian Muscum, Perth

# PREVIOUS WORK

There is surprisingly little in the literature concerning the fossil emus of Australia (see Table 1). The first reference to a specimen supposedly related to emus was, in fact, a moa, 'Dinornis queenslandiae', described by De Vis (1884) from the Darling Downs, Queensland. Some later workers considered this specimen (e.g. Hutton 1893, Miller 1963) to be related to the emus and cassowaries. Scarlett (1969), however, found the fossil could be assigned to *Pachyornis elephantopus*, probably collected from a midden on South Island, New Zealand, and thus it is not a valid Australian record, and certainly not an emu.

In 1888 De Vis described a new species of emu, Dromaius patricius, from a proximal end of a right tibiotarsus (QM F5547) and the distal end of another tibiotarsus (QM F5548). In the same paper he provisionally referred a left coracoid (QM F1120) to the same species. These three fossils were from King Creek, Darling Downs, in south-eastern Queensland, De Vis (1892) considered the whole of the Darling Downs sediments to be much the same age, but it is now known that these fossil-bearing deposits represent a range of ages. The Chinchilla fauna is likely to be of Late Pliocene age. On the other hand, the Darling Downs fauna of the eastern part of the Downs, including King Creek, is of Late Pleistocene age (Woods 1960, Stirton et al. 1968, Rich 1979). Later De Vis (1892, 1905) also referred a femur fragment, three tarsometatarsi, and a partial synsacrum (QM F5549) to D. potricius. The referral of the synsacrum is especially noteworthy. De VIs considered that because of its size, the fragment must have been from a cassowary or an emu, but: fas no extinct cassowary is known yet in Australia, it seems almost necessary to attribute the present fossil to the emu D. patricius' (De Vis 1905: 25).

In 1892 De Vis set up another species of emu, Dromaius gracilipes, based on a distal left tarsometatatsus (QM F1142). In the description De Vis omitted to note the location from which the specimen was collected, but the museum label associated with the specimen indicates that it was from the Darling Downs. In this article De Vis (1892) also described a supposed kiwi, 'Metapteryx b(frons', again without giving a location.

Spencer (1906) described D. minor of King Island, Bass Strait, Tasmania. The previous existence of a separate species of emu on this island was almost simultaneously made by Legge (1907), but he withdrew the name. *D. minor* was tedefined by Spencer & Kershaw (1910) as more specimens became available, and recently the taxonomic status of this species has been discussed by Parker (1984).

The status of the extinct Tasmanian emu is an as yet unresolved problem. Emus were introduced from the mainland in the 1800s, and interbreeding may have occurred (Howchin 1926). Le Souef (1903) gave the Tasmanian emu the specific name *D* diemenensis. Ridpath & Moreau (1966) considered it a subspecies of *D*, novaehollandiae. The only fossils and recent specimens of *D* diemenensis collected allye which are known to exist include a femur, a synsacrum, three tibiotarsi, two tarsometatarsi, a cervical vertebra, and a leg lacking the femur and part of digit 11 (all at QVM) (Scott 1924, 1932), and three eggs (in private collections) (Campbell 1900, Le Souef 1903, Spencer & Kershaw 1910, Dove 1926).

Anderson (1937) described an emu sternum, which is much thicker than those of the living *D. novachollandiae*, from the Wellington Cayes, New South Wales. He suggested it might possibly belong to *D. patricius*.

Miller (1962) restudied Casuarius lydekkeri, discussed earlier by Rothschild (1911). The type of the species is a distal right tibiotarsus (AM MF1268). The type locality has been variously given as Queensland, Cooma and Wellington Caves (Miller 1962), but its provenance is uncertain. Its preservation, however, is very unlike that of fossils from Wellington Caves, It is clearly a cassowary, however, and not an emu.

Miller (1963) described a new species of emu Dromiceius (=Dromatus) ocypus based on an essentially complete right tarsometatarsus (SAM P13444) from the Pliocene Mampuwordu Sands. Palankarinna fauna, Lake Palankarinna, South Australia. It is smaller than D. novaehollandiae. The tarsometatarsus Is evidently the one referred to by Miller In Stirton et al. (1961) as a new species of emu with 'proportions of the bone... intermediate between those of the emu and the cassowary'.

Miller also assigned four phalanges (UCMP 56849, 60563, 94679, 94680) from Lake Kanunka (UCMP V-5772, Katipiri Sands or possibly Tirarl Formation) to the Dromornithidae, possibly Genyornis newtoni (Stirton et al. 1961). As noted by Rich (1979), however, they actually belong in the genus Dromalus: Thus, no dromornithids are known from the Pliocene-Pleistocene Lake Kanunka fauna, and this adds another record for emus.

Rich (1979) refers a left femur (SAM P17104), from Brother's Island, South Australia to Genyornis newtoni, but it conforms in all respects to Dromaius and should be transferred to that taxon.

Locality	Fossil Elements	Rock	Fauna	Age	References
Leaf locality, Lake Ngapakaldi, South Australia	Tmt., d Tib., Pes Dromaius gidju	Wipajiri Fm.	Kutjamarpu	Miocene	Stirton <i>et al.</i> 1967, 1968; Rich 1979.
Bullock Creek, Northern Territory	Tmt., Tib. Dromaius sp.	Camfield beds	Bullock Creek	Late Miocene	Rich 1979
Alcoota (including Rochow locality), Northern Territory	Tmt. frags., Phs. Dromaius sp.	Waite Fm.	Alcoota	Late Miocene	Woodburne 1967, Stirton <i>et al.</i> 1968, Rich 1979, Rich <i>et al.</i> 1982
Lawson-Daily Quarry, Lake Palan- karinna, South Australia	Tmt. Dromaius ocypus; Tib., F. Dromaius cf. ocypus	Mampuwordu Sands	Palankarinna	Pliocene	Miller 1963, Rich 1979
Lake Kanunka, South Australia	F., Ph., R., Tib., V. Dromaius novae- hollandiae, Dromaius sp.	Katipiri Sands	Kanunka	Late Pliocene or Early Pleistocene?	Rich 1975, 1979
Chinchilla, Queensland	Syn., F., Tmt. Dromaius novae- hollandiae	Chinchilla Sands	Chinchilla	Early to Middle Pliocene	Woods 1960, Stirton <i>et al.</i> 1968, Rich <i>et al.</i> 1982
Darling Downs, Queensland	Cor., F., Tib., Tmt. Dromaius novae- hollandiae	Unnamed	Darling Downs	Pleistocene	Woods 1960, Rich 1975, 1979
King Creek, Queensland	Dromaius novae- hollandiae	Unnamed	King Creek	Late Pleistocene	Baird 1986
Thorlindah, Paroo River, Queensland	Tib. Dromasius novae- hollandiae	Unnamed	Unnamed	Pleistocene	Etheridge, 1889, Rich 1975, 1979
Bingara, New South Wales	V., Syn., Tib. Dromaius novae- hollandiae, Dromaius sp.	Unnamed	Bingara	Pleistocene	Anderson 1889, Rich 1975, Marcus 1976
Lake Menindee, New South Wales	Ph., Tib. Dromaius novae- hollandiae	Unnamed sand lunette	Unnamed	Late Pleistocene	Tedford 1967
Lake Tandou, New South Wales	Dromaius sp.	Unnamed	Unnamed	Pleistocene	Rich 1975
Wellington Caves, New South Wales	Tib. Casuarius lydekkeri; St., Tib., Tmt. Dromaius novae- hollandiae, Dromaius sp.	Unnamed cave sediments	Unnamed	Quaternary	David 1950, Rich 1979, Dawson pers. comm.
Wombeyan Quarry Cave, New South Wales	Tib., Tmt. Dromaius novae- hollandiae	Unnamed cave sediments	Unnamed	Late Pleistocene	Hope 1971, Rich 1975
?Baldina Creek, near Burra, South Australia	F. Dromaius sp.	Unnamed	Unnamed	Quaternary	S.A.M. Museum label
Brothers Island, South Australia	F. Dromaius novae- hollandiae	Unnamed aeolianite	Unnamed	Quaternary	Rich 1975, 1979

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Cooper Creek, (includes Katipiri Waterhole and Wurdulumankula), South Australia	F,M Tmt., Syn., V. Dromaius sp. Dromaiinae	Katipiri Sands	Malkuni	Pliocene- Quaternary	Stirton <i>et al.</i> 1961, Rich 1975
Kangaroo Island, South Australia (Several localities)	Sk Dromaius baudinianus	Unnamed	Unnamed	Quaternary	Morgan & Sutton 1928, Rich 1975, Parker 1984
Lake Callabonna (lower stratigraphic level), South Australia	C., Syn., V., F., Tib. Dromaius novae- hollandiae	Millyera	Lake Callabonna	Pleistocene	Stirling & Zeitz 1900, Rich 1975, 1979
Lake Kittakittaooloo, South Australia	Tmt. Dromaius novae- hollandiae	Katipiri Sands	Malkuni	Quaternary	S.I.A.M. Museum label
Naracoorte (Henschkes Bone Dig and Victoria Fossil Cave) South Australia	M., V., R., Hum., Syn., F., Tib., Tmt., phs. Dromaius novae- hollandiae, Dromaius sp.	Unnamed cave sediments	Unnamed	Pleistocene	van Tets & Smith 1974
Salt Creek, South Australia	F. frag. Dromaius cf. novae- hollandiae	Unnamed	Unnamed	Quaternary	Rich 1975
Warburton River, South Australia (includes Green Bluff locality and Kalamurina).	Syn., Tib., Tmt. Dromaius sp.	Katipiri Sands	Malkuni	Quaternary	Rich 1975
Bone Cave, Western Australia	Tib., Tmt. Dromaius novae- hollandiae	Unnamed cave sediments	Unnamed	Quaternary	
A cave north of Moore River, Western Australia	Tmt. Dromaius novae- hollandiae	Unnamed	Unnamed	Quaternary	Rich (unpublished, 1971, field notes)
Irishtown, Tasmania	Tib. Dromaius diemenen- sis. Needs review	Unnamed	Unnamed	Quaternary	Scott 1924
King Island, Bass Strait, Tasmania	Sk. Dromaius minor	Unnamed sand rock and dunes	Unnamed	Quaternary	Spencer 1906, Spencer & Kershaw 1910, Jennings 1959, Parker 1984, Rich 1975
Mole Creek, Tasmania	Tib. Dromaius diemenensis. Needs review	Unnamed	Unnamed	Quaternary	Scott 1932
Moybray Swamp, Smithton, Tasmania	Syn., V., F., Tib., tmts. Dromaius diemenensis. Needs review	Unnamed	Unnamed	Quaternary	Scott 1932
Scotchtown Cave, Tasmania	C. Dromaius diemenensis. Needs review	Unnamed	Unnamed	Quaternary	Gill & Banks, 1956

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Locality	Fossil Elements	Rock	Fauna	Age	References
Lancefield, Victoria	Tib., Tmt., Ph. Dromaius novae- hollandiae	Unnamed	Unnamed	Pleistocene (26 000 B.P.)	Gillespie et al. 1978
McEachern's Cave, Victoria	Many skeletal elements Dromaius novae- hollandiae	Unnamed	Unnamed	Quaternary	McNamara pers comm.
Buchan Caves, Trogdip Cave area, Victoria	Tmt. Dromaius novae-hollandiae	Unnamed	Unnamed	Quaternary	Rich 1975.

The bird remains in the Riversleigh fauna (Carl Creek Limestone) identified only as close to 'Dromiceius' in Tedford (1967) have been determined by Rich (1979) to belong to a dromornithid, Barawertornis tedfordi, and thus are not a record of emu.

# STRATIGRAPHY (see Table 1)

Only a few fossil sites producing emus have been found thus far, and most are of Pleistocene age. Fossils of a new species, Dromaius gidju, proposed in this paper, have been found at the Leaf Locality (UCMP V-6313) on the eastern shore of Lake Ngapakaldi, eastern Lake Eyre sub-basin, South Australia (Stirton et al. 1967). The sediments that outcrop here, known as the Wipajiri Formation, contain the Kutjamarpu fauna. Diprotodontid marsupials in this fauna are considered more primitive than those in the Beaumaris, Palankarinna, and Alcoota faunas, and have closest affinities with forms in the older Ngapakaldi fauna, known from localities listed in Stirton et al. (1968), in the Lake Eyre sub-basin and thought to be of medial Miocene age (Rich et al. 1982).

The Camfield beds at Bullock Creek (Bullock Creek fauna), Northern Territory, of probable Late Miocene age, have produced *Dromaius* sp. currently under study by P. V. Rich.

The Rochow locality (UCMP V-6349) at Alcoota, Northern Territory, near Alice Springs, has produced *Dromaius* remains that may be Miocene in age. But, as discussed by Rich (1979), the Waite Formation, which contains the Alcoota fauna, is not well dated at present. The diprotodont marsupials from this locale suggest a date younger than that represented by the Kutjamarpu fauna but older or contemporaneous with the Hamilton fauna. An unnamed rock unit containing the Hamilton fauna is capped by a basalt, which has been dated as  $4.35 \pm 0.01$  m.y. B.P. (or Early Pliocene) by Turnbull *et al.* (1965) and Turnbull & Lundelius (1970). The sequence is underlain by marine sediments of the Grange Burn Formation assigned to the Kalimnan stage. At present Alcoota is viewed as Late Miocene in age.

Dromaius ocypus was recovered from the Lawson-Daily Quarry (or Lawson Quarry; UCMP V-5769) at Lake Palankarinna, eastern Lake Eyre Basin, South Australia (Miller 1963). The enclosing rocks, the Mampuwordu Sands, contain the Palankarinna fauna, and are overlain by the Tirari Formation and the Late Pliocene or Early Pleistocene Katipiri Sands containing the Malkuni fauna at Lake Palankarinna. An age of Middle to Late Pliocene is established by marsupial fossils, in particular Zygomaturus, which are more advanced than zygomaturines from Awe, Beaumaris, and Alcoota and yet more primitive than Pleistocene forms (Stirton et al. 1968).

Lake Kanunka (UCMP V-5772) in the eastern Lake Eyre sub-basin, South Australia, has also yielded *Dromaius* fossils. The Katipiri Sands or possibly Tirari Formation (see Rich 1979: 61) contains the Kanunka fauna dated as Pliocene or Early Pleistocene (Stirton *et al.* 1961, Rich *et al.* 1982, Tedford pers. comm. 1985).

The Chinchilla locality, south-eastern Queensland (Chinchilla Sands, Chinchilla fauna) also contains *Dromaius*. Several elements of the marsupial fauna appear more primitive than those in the Pleistocene eastern Darling Downs, and Woods (1960) assigned it a Pliocene age. Rich *et al.* (1982) consider Chinchilla to be Early to Middle Pliocene in age.

The distal part of a tarsometatarsus (AM F 58087) of an emu was found in the Australian Museum's 'old collection' and labelled 'mixed plus some from Lord Howe Island'. The fossil is very incomplete and appears to be from a juvenile individual. There are no reliable stratigraphic or locality data available for this form.

All of the other known fossiliferous sites producing emus are Pleistocene in age. For these

Pleistocene sites, as might be expected, some dates are better established than others. Deposition, for instance, of the Darling Downs sediments in Queensland may have occurred at several different times (Rich 1979) during the Pleistocene, and definite ages for specific sites are difficult to determine.

Thorlindah, on the Paroo River, Queensland, is thought by Rich (1979) to be 'probably Pleistocene ... the bird remains were collected along with fragments of 'kangaroos' and *Diprotodon* (Stirling & Zeltz 1900: 44) in a well 20 feet deep'. *Diprotodon* appears to be restricted to the Pleistocene in all precisely dated situations. Emu material indistinguishable from the living forms is known from Thorlindah.

Vertebrate fossil-bearing localities at Lake Menindee adjacent to the Darling River and its major anabranch, western New South Wales, have been radiocarbon dated at 26 300  $\pm$  1500 B.P. and 18 800 B.P. (Tedford 1967). Fossils of Diprotodon, Thylacoleo. Phaseolonus, Protemnodon and macropodids have been recovered. UCMP localities V-5371, V-7185, V-67186 and V-67187 have produced Dromahus fossils, Hope (1978) discusses the stratigraphy of the Menindee area in some detail, with reference to the problem of dating the Pleistocene megafauna extinctions. At present the emu fossils from Menindee appear to be Late Pleistocene in age.

At Lake Tandou, New South Wales, several Dromaius fossils were found in archaeological excavations. Hope (pers. comm.) states that: 'there is now a reasonable stratigraphy for the lunette [at Lake Tandou], and a lot more dates; the oldest are in the order of 22 000-25 000; and lie at the base of the uppermost stratigraphic unit. The problem .... is in working out where Harry's [Harry Allen, who collected the specimens while doing research toward a Ph.D. thesis] material came from'. Tentatively, a Pleistocene age seems appropriate for these fossils.

Bingara in New South Wales has produced vertebrae and a libiotarsus of *Dromaius*. The bone bed occurs in a fluviatile clay deposit about 39-90 cm thick on the western side of Myall Creek, Remains of *Diprotodon* indicate a Pleistocene age (Anderson 1889).

Also in New South Wales, the Wombeyan Quarry Cave has yielded *Dromaius* fossils. This is not the same cave as Broom Cave or Guineacor Cave, also in the vicinity of Wombeyan. The Wombeyan Quarry Cave has not been radiocarbon dated, but Hope (1982) believes that it is of Late Pleistocene age. It seems likely that the quarry deposit is older than the 'Broom breecia', but both appear to be of Late Pleistocene age. Other fossils recovered from Wombeyan Quarry Cave include *Protemnodon*, Sthenurus, Zygomaturus, Palorchestes, Thylacoleo curnifex, Sarcophilus Ianiarius, and Progura gallinavea.

There are several bone producing caves in the Wellington Valley area of New South Wales. Different levels and different caves may have trapped animals at various times in the Pleistocene to Recent, perhaps even prior to this (L. Dawson pers. comm.) depending on when they were opened and rescaled (David 1950, Tedford 1967), Emu fossils have been recovered from caves in this area.

Rich (1979: 58) states that Dromaius remains were recovered from Cuddle Springs (Mara Creek, SSE of Brewarring, 16 km ESE of Gilgoin), New South Wales, Anderson & Fleicher (1934) do not mention Dromains in their, admittedly incomplete, list of fossils recovered from this site. Wilkinson (1884) stated that: 'bones of Diprotodon, Sthenurus, Macropus (itan, large wombats, large birds probably emus, crocodiles and a gigantic carnivorous lizard. Notiosaurus .... are found only within a few yards of the centre of the spring'. Unfortunately, he does not describe or figure these bones, and the large birds may be Genvornis, specimens of which were later recovered by Anderson and Fletcher. MM F 19420, unlabelled when found in an old collection. has the style of preservation (suggesting) that it comes from Cuddie Springs' (Pickett pers. comm.) but is too large to be Dromaius. It appears, instead, to be the internal condyle of a tibiotarsus of a dromornithid, perhaps Genyornis. We have been unable to relocate the specimens Rich (1979) assigned to Dromaius.

Two Pleistocene cave deposits producing Dromaius fossils are known in Western Australia. A cave north of East Moore, Western Australia, has produced a tarsometatareus of a juvenile emu (unregistered WAM). Bone Cave, near Jewel Cave, has produced an emu tibiotarsus and tarsometatarsus.

Four Pleistocene Dromaius localities are known from Tasmania. Scott (1924, 1932) reported a tibiotarsus from Irishtown, a tibiotarsus from Mole Creek, and several elements (a synsacrum, femur, tibiotarsus, two tarsometatarsi, and a cervical vertebra) from Mowbray Swamp, near Smithton, in western Tasmania. The Mowbray Swamp fossil site has been radiocarbon dated at greater than 37 780 B.P. (Gill & Banks 1956). Another Mr Scott found bones of the Tasmanian emu at Scotchtown Cave in association with "Nototherium tasmanicum", Thylacoleo carnifex, and Palorchestes (Gill & Banks 1956).

Dromaius minor is known from the Bass Strait island, King Island, 'lasmania. Anderson (1914) was of the opinion that the original fossil matrix was a fairly hard, coarse, red-brown sand rock of shallow marine origin. Jennings (1959) stated that the fossils occurred in windblown sand dunes of Pleistocene to Recent age and that finds from different geological horizons had likely been brought together by winnowing. Separate from the King Island form, the now extinct *Dromaius baudinianus*, is known from Kangaroo Island (Parker 1984).

Several localities along the south coast of Kangaroo Island (Cape du Couedic, Kelly Hill, Eleanor River, and The Brecknells) have produced fossil material (Morgan & Sutton 1928). Rich (1975) states that the age is Pleistocene.

Three Victorian sites, all Pleistocene in age, have produced fossil emus. A partial tarsometatarsus is known from Trogdip Cave, part of the Buchan Caves said by Rich (1975) to be Pleistocene because of the nature of the marsupial fauna also preserved in it.

Many fossils of the Australian megafauna have been recovered from a swamp near Lancefield, Victoria. As well as emus (less than 1% of the bones), *Macropus giganteus, Protemnodon, Sthenurus, Diprotodon*, and a dromornithid, probably *Genyornis*, were found. A sample of the bones themselves was radiocarbon dated at 19 800  $\pm$  450 B.P., while charcoal in the channel fill in and upon which the fossil deposit rests provides a maximum age for the bones of 26 000  $\pm$  500 B.P. (Gillespie *et al.* 1978).

A third Victorian site which has produced emu fossils is McEachern's Cave in western Victoria. According to Wakefield (1967, 1969), due to the funnel shape of the entrance the cave has acted as a death trap for terrestrial animals. Gravitational movement, movement of trapped animals and water action were responsible for considerable mixing of cave sediments. The fossils are Late Pleistocene to Recent in age. A sample of mammal bones from the top layer of the Pleistocene sediments gave a radiocarbon date of 15 200  $\pm$  320 B.P. Extinct Pleistocene species found in the cave include *Sarcophilus laniarius, Zygomaturus trilobus, Thylacoleo carnifex, Sthenurus* spp. and *Protemnodon* cf. brehus.

The remaining sites from which fossil emus have been recovered are all South Australian. From Brothers Island, Coffin Bay, about 50 km WNW of Port Lincoln, a femur fragment SAM P17104, referred to *Genyornis newtoni* by Rich (1979) but actually *Dromaius*, was found in an unnamed aeolianite of sand and shells. As similar deposits on the island have produced *Sthenurus* cf. *brownei* (Tedford in Rich 1979), a Pleistocene age is indicated.

A number of Pleistocene localities collected by J. W. Gregory (1906) and later by joint expeditions from the University of California and the South Australian Museum, occur in the eastern Lake Eyre basin. The fossils were found as 'float' or in place in the Katipiri Sands, which contain the Malkuni fauna. Also collected by Gregory and later expeditions of the University of California and the South Australian Museum, are several localities on the Warburton River, including Green Bluff Locality (UCMP V-5771), Lookout Locality (UCMP V-5776) and Kalamurina. The Warburton River is in the eastern Lake Eyre sub-basin, and has produced fossils from the Katipiri Sands. A Smithsonian Institution-American Museum (SIAM) expedition in 1970 recovered a tarsometatarsal fragment (SIAM 75) of an emu from the Katipiri Sands (Malkuni fauna) at Lake Kittakittaooloo.

The Smithsonian Institution-American Museum Expedition and later a Museum of Victoria-Australian Army Expedition also recovered a number of *Dromaius* fossils from the lower level of Lake Callabonna in South Australia. This stratigraphic unit producing the emus also contained *Genyornis newtoni*, *Diprotodon optatum*, *Phascolonus gigas*, *Sthenurus*, *Protemnodon*, and *Macropus* (Stirling & Zeitz 1900, Rich 1979) and has been dated at greater than 40 000 B.P. (Tedford 1967), but sometime during the Pleistocene.

An incomplete femur (SAM P17103) bearing the museum label: '?Genyornis. Pleistocene locality unknown, possibly Baldina Creek near Burra, South Australia' is actually Dromaius. If the location is in fact Baldina Creek, a Pleistocene age is suggested by the occurrence of known Genyornis newtoni (Rich 1979) and Diprotodon at this site (Stirling & Zeitz 1900).

Several fossils of *Dromaius* were collected near Burra, South Australia by Mr R. E. Ireland and forwarded by the police department on 12 March 1935 to the South Australian Museum. They were found in a sandhill in association with Aboriginal (*Homo sapiens*) bones, SAM A25805 (information from museum label). The Aboriginal remains suggest a Pleistocene to Recent age.

Two caves near Naracoorte (about 320 km SE of Adelaide near the Victorian border), South Australia, have produced *Dromaius*: Victoria Fossil Cave (van Tets & Smith 1974) and Henschke's Bone Dig. Sediments producing the fossils in Henschke's Bone Dig have been radiocarbon dated at about 33 800 B.P. (van Tets 1974). Smith (1971) stated that the bones in Victoria Fossil Cave are most abundant in the top 15 cm of the damp, friable, light brown earth forming the floor of the cave. She also states that the abundance of sthenurines, diprotodontids, and *Thylacoleo* suggests that the deposit was formed sometime during the Pleistocene and sealed before the Recent. Wells *et al.* (1984) provide a complete discussion of current dates from this site.

#### SYSTEMATICS

Only those features exhibited by the fossil specimens are discussed. For measurements see Table 2.

# Family CASUARIIDAE Brisson

Members of the Casuariidae have a ptervgoid that is inflated where it contacts the palatine; a palatine with a short shaft and an expanded medial plate; a long vomer; a palate that lies ventral to the parasphenoid rostrum and makes contact with the braincase only at the basipterygoid processes; maxillopalatines that are cone-shaped and open posteriorly; the cervical vertebrae are anteroposteriorly compressed; the atlas possesses lateral spines or occasionally complete vertebrarterial canals; the sternum is longer than wide with lateral margins concave laterally and has short, dorsallydirected sternocoracoidal processes and no sternal notches; the costal margin forms about 50% of the lateral margin; the antitrochanter of the synsacrum is located at the anteroposterior mid-point of the synsacrum; the ilium, ischium and pubis are subequal in posterior extent; neither the pubes nor the ischia are fused posteriorly along the mid-line; the ischium is deeper than the pubis; the ilium dorsal to the acetabulum is deep; the trochanter and head of the femur are subequal in proximal extent; the external condyle extends only moderately distal to the internal condyle; the popliteal fossa is elliptical and of moderate width; the distal depth and width of the femur are subequal; the posterior margin of the proximal articular surface is highly concave anteriorly; the external condyle and fibular condyle are subequal in breadth or the fibular condyle is broader; the cnemial crests of the tibiotarsus are little compressed mediolaterally; the inner cnemial crest extends far proximally to the proximal articular surface; the external articular surface extends far laterally; the margin of the external condyle is semicircular in lateral view; the tibiotarsus lacks a supratendinal bridge and also lacks an intercondylar eminence; the hypotarsus of the tarsometatarsus is narrow and centrally located; the hypotarsus extends decidedly further proximally than the intercotylar prominence; the internal cotyla is deeper than the external; the posterior shaft surface is deeply grooved; the anterior metatarsal groove is deep and extends the length of the shaft; trochlea IV extends distal to trochlea II; trochlea III extends distal to trochleae II and IV; the phalangeal count for digits II, III, IV is 3-4-5; of the proximal phalanges that of digit III is longest; that of digit IV is shortest; the unguals are generally claw-like, except for the elongated ungual of digit II in Casuarius.

# Subfamily DROMAIINAE Vieillot

Within the Casuariidae there are a number of characters which reliably distinguish Dromaius from Casuarius, the only other member of the family. In Dromaius the mandible is broad and rounded distally, not narrow and pointed distally; the mandibular articulation of the quadrate is stepshaped, with the external facet decidedly more excavated (in Casuarius the facets of the mandibular articulation of the quadrate are subequal); the pterygoid is not excavated dorsally; and the palatine and vomer are decidedly shorter than in Casuarius; the semicircular notch in the prearticular surface of the atlas is shallow and narrow, not deep and broad; the axis is longer, and the hypapophysis not as deep as in Casuarius; the cervical vertebrae possess long, not short, styloid ribs, which come to a point distally, and are not rounded; the neural canals and vertebrarterial canals are small; the excavation of the neural arch posterior to the prezygapophysis is shallow (from the eighth cervical posteriorly in *Casuarius* the excavation of the neural arch is deep); the thoracic vertebrae are similar to those of Casuarius, but the neural canals are smaller; the neural canals of the caudal vertebrae are small, with an elliptical cross-section, whereas in Casuarius the neural canals are large and triangular in cross-section; the sternum is only slightly longer than wide, not much longer than wide as in Casuarius; the costal processes lie in an almost horizontal plane, whereas in *Casuarius* they lie on a downward curve (antero-posteriorly); the sterno-coracoidal processes are moderately long, not very short as in Casuarius; the coracoidal sulci are short and overlap medially, whereas they are long and do not overlap in Casuarius; the body of the sternum is weakly concave dorsally, but in Casuarius it is strongly concave dorsally; the depth of the sternum anteriorly is shallow, not deep; the costal margin is long, whereas in *Casuarius* it is shorter; the supratrochanteric ridge is broader; the pre-acetabular synsacrum tends to be shorter than the post-acetabular synsacrum in Dromaius while the opposite condition exists in *Casuarius*; proximally and posteriorly the femur bears a large pneumatic foramen, lacking in Casuarius; in anterior view, the external condyle extends decidedly further proximally than the internal condyle, while the two condyles are subequal in anterior proximal extent in Casuarius; in medial view, the internal condyle is semicircular in outline, while in Casuarius it is triangular; the diameter of the head and the minimum diameter of the shaft at its proximo-distal mid-point are equal, whereas in Casuarius the head diameter is less than the shaft diameter; the shaft is almost straight, being more curved in Casuarius; the proximal extent of the cnemial crest is not as great as in *Casuarius*; anteriorly the external

condyle is rounded proximally, and it extends further proximally and is more pointed in Custarius; above the anterior intercondylar fossa is a small ridge trending dorsally and laterally from the mid-line and ending in a small foramen, while in Cosuarius this tidge is absent, but the foramen still exists; the tarsometatarsus and tibiotarsus are subequal in length, unlike in Casuarius in which the tarsometatarsus is decidedly shorter; the second trochlea is much more reduced than in Castlurlus; the intercotylar prominence is low and tends to be flat, while in Casuarius the intercotylar prominence is higher and convex dorsally; a distal foramen, which completely penetrates the tarsometatarsus (antero-posteriorly), and a groove (occasionally a completely roofed-over forainea) running proximodistally, are present, both absent in Cusuarius, the condules of the phalanges of the foot tend to be greatly divergent plantarly; in Casuarius the condutes tend to be only moderately divergent plantarly; in distal view, the intercondylar fossa tends to be only slightly notched in a step-shaped fashion dorsally, while in Castlarius this notch tends to be deeper and more V-shaped; the ungual of digit III is longest, and that of digit IV shortest, while in Casuarius the ungual of digit II is longest, and that of digit IV shortest.

### Dromains novaehollandise (Latham)

#### Npe

Casuarius novaehollandiae (Latham)

Type Locality

New Holland (Sydney, New South Wales, Australia) (Table 1).

### **Measurements**

Tables 2-13.

### Referred Fossil Material

Bingara, New South Wales — V, MM F16786, dotsal vertebra (V.24-26?), neural spine, pre- and postzygapophyses, diapophyses and prearticular surface damaged; MM F16797, dotsal vertebra (V.24-26?), neural spine and diapophyses not preserved. *Tile.*, MM F16775, distal end and distal half of shaft. Pleistocene.

Bone Cave (near lowel Cave), Western Australia - Tib., WAM 68.5.34 (in part), shaft only. Tht., WAM 68.5.34 (in part), shaft only. Quaternary.

Brothers Island, South Australia —  $E_0$ , SAM P17104, proximal end and proximal two-thirds of shaft, head and trochanter damaged. Quaternary.

Chinchilla, Queenstand — Thus. QM F1143 (in part), third trochlea only.

Cooper Creek, South Australia — Syn., UCMP 56333, acetabular complex, (site 2, UCMP V5378). R., HM B775/869, entire, (Lower Cooper, locality 3). Tint., UCMP 56313, distal end, fourth trochlea not preserved, (site 3, UCMP V5379). Late Pliocene or Early Pletstocene.

Darling Downs, Queensland — F, QM F1143 (in part), distal, popliteal fossa region only (eastern Darling Downs). *Tib.*, AM A9713, proximal, see Figure 1; QM F5547, proximal, figured (De Vis 1889); QM F5548, distal, figured (De Vis 1889); QM F1652, proximal end, most of cnemial crests not preserved, (Condamine River, near Dalby). *Tmt.*, QM F1121, proximal frag.; QM F1135, figured (De Vis, 1892), distal, juvenile; QM F1142, distal frag.; QM F1143 (in part), distal end (castern Darling Downs). Pleistocene.

Lake Callabonna, South Australia — AMNH 9678. V., second cervical, posterior left side; third cervical, left side: fourth cervical (articulates with third cervical), neural spine and ribs not preserved; sixth cervical?, ribs and right side postarticular surface not preserved; seventh cervical?, (articulates with sixth cervical), ribs and right side prezygapophysis not preserved; ninth cervical?, postarticular surface, ribs, right side postzygapophysis not preserved. SIAM 61. St., fragments, AMNH 9677. F., distal end, internal condyle damaged. AMNH 9676. Tib., entire, see Figure 2. Pleistocene.

Lake Kamunka, South Australia — V., UCMP 56855, dorsal vertebra (V.22 or 23), (UCMP 5772). F., UCMP RHT1064, trochanter, condyles, and head partly eroded and crushed, (site 1, UCMP V5772). T/b., UCMP 56845, distal end, most of internal condyle not preserved and remainder highly croded (UCMP V5772). Ph., UCMP 56849, first phalanx, second digit, (UCMP V5772); UCMP 94679, first phalanx, third digit; UCMP 94680, second phalanx, third digit (UCMP V5772). Late Pliocene or Early Pleistocene.

Lake Menindee, New South Wales — Eggshell, UCMP 55948. Tib., UCMP 53825, two distal tibiotarst with the same number. Tinl., UCMP 53835, distal end most of third trochlea and second and fourth trochleae not preserved. Ph., UCMP 53832, dark colour (presumably burnt), first phalanx, second digit, distal end; ungual phalanx, second or fourth digit; first phalanx, second digit, proximal end; second phalanx, fourth digit (UCMP V5371), UCMP 53833, first phalanx, fourth digit and ungual (site II, V67185); UCMP 55983, first and second phalanges, third digit (UCMP V67186), Late Pleistocene

Lancefield, Victoria — 77b., NMV P43037, distal shaft; NMV P43041, distal shaft, juvenile: NMV P44011, entire but articular surface worn; NMV P150013, distal, 7mL, NMV L5, distal; NMV P44012, proximal articular surface croded; NMV P44013, hypotarsus eroded; NMV P44014; NMV P44015, proximal articular surface worn, second and fourth trochleae not preserved; NMV P44016, proximal articular surface worn; NMV P44017, distal shaft; NMV P44018, distal; NMV P44019, distal; NMV P48392, second and part of third trochleae not preserved; NMV P150014, distal, fourth trochlea not preserved. *Ph.*, NMV P43199, first phalanx, third digit, articular surfaces worn; NMV P43200, second phalanx, third digit, proximal end. Late Pleistocene, 26 000 B.P.

McEauhern's Cave, Victoria - C., NMV P157345, posterior fragment: NMV P157350, lower aw, distal; NMV P157353, posterior fragment. V. NMV PI57346, 21st or 22nd vertebra, neural spine, diapophysis, right side prezygapophysis, part of centrum and prearticular surface not preserved; NMV P175349, 23rd pr 24th vertebra, neural spine, pre- and postzygapophyses not preserved, postarticular surface worn; NMV P157351, seventh cervical?, juvenile, ribs not ankylosed; NMV PIS7352, 11th, 12th or 13th cervical, juvenile: NMV P157359, third cervical, right side rib not preserved; NMV P157364, 25th or 26th vertebra, left side of centrum with prezygapophysis and diapophysis, but postarticular surface not preserved; NMV P157367, 20th or 21st vertebra, diapophysis, part of neural arch, postzygapophyses, and right side prezygapophysis only, juvenile; NMV P157368, about 11th cervical, prearticular surface worn, left side prezygapophysis and ribs (not ankylosed) not preserved, juvenile; NMV P157369, 22nd to 26th vertebra, right side of centrum only, juvenile. St., NMV P157347, incomplete; NMV P157355, entire. Syn., NMV P157361, fragment. Tib., NMV P157356. proximal; NMV PJ57357, distal; NMV P157360, distal; NMV P157365, proximal, Fib., NMV P157363, proximal end. Thil., NMV P157344, distal, trochleae not preserved. Quaternary.

Cave north of Moore River, Western Australia — Tht., WAM-190 unregistered, (not seen, data from Pat Rich's 1971 field notes). Quaternary.

Naracoorte, (Henschke's Bone Dig and Victoria Fossil Cave), South Australia - C., SAM P17834, lower jaw, distal end only, (Henschke's A3, 40"). V., SAM P17589, 16th cervical, ribs not preserved: SAM P18246, fourth cervical; SAM P18247, 22nd to 24th vertebra, part of centrum and left side diapophysis, (Henschke's); SAM P18673, 15th to 17th cervical? vertebra, prezygapophyses and centrum damaged, (Henschke's area X4, depth 17"); SAM P18830, 26th vertebra, prezygapophyses, prearticular surface and diapophyses damaged, (Henschke's area X6, 15-30 cm). Syn., unregistered SAM; SAM P16501, acetabular complex only, (Victoria Fossil Cave, 0-10-R10-0-12"), see Figure 3; SAM P17767, parts of illum, ischia and pubes not preserved, (Henschke's A3, 39-42"); SAM P18100, distal right ischium only. (Henschke's A1, 33-36").  $E_{\rm s}$  SAM P22812 (in part), condyles badly eroded; unregistered SAM, internal condyle damaged. Tib.,

SAM P17149, distal end, internal condyle worn; SAM P18829, distal, part of condyles not preserved, (Henschke's area X6, 0-15 cm). Tint., SAM P17816, distal, (Henschke's A1, 30-33'); SAM P18693, 2 pieces, proximal, with articular surface badly eroded, and distal (Henschke's area A4, 150 cm, western wall), Ph., SAM P18059, first phalanx, second digit (Henschke's area A3, 33-36''); SAM P18248, second phalanx, third digit, (Henschke's); SAM P18249, first phalanx, fourth digit, (Henschke's); SAM P18252, first phalanx, fourth digit, (Henschke's). Pleistocene,

Salt Creek, South Australia — E, SAM P17101, proximal shaft only, but head and part of trochanter not preserved. Quaternary.

Thorlindah, (Parno River), Queensland — Tib., MMF 12074, figured (Etherldge 1889), a cast (AM LSI6) has been made, distal end, condyles worn. Pleistocene.

Trogdip Cave, Buchan Caves, Victoria - Tint., NMV P157343, shaft only. Pleistocene.

Warburton River, South Australia — V., UCMP 56642, 21st or 22nd vertebra, centrum only (Green Bluff locality, UCMP V-5775). Syn., UCMP 56647, fragment, fused sacral vertebrae only. F., HM B801/934, distal, most of internal condyle not preserved, (Kalamurina), see Figure 4. Tint., SAM P13118, distal end, second trochlea not preserved. (Stony crossing of Warburton, Six road miles west of new Kalamurina Station.) Quaternary.

Wellington Caves, New South Wales — Th., AM 'B', distal end, external condyle missing; AM F10949, distal half, (J. Mahoney, in a note on the back of the museum label, disputes this locality). *Tint.*, unregistered AM, proximal articular surface badly worn; AM 'C'; proximal; AM F18935, distal end and part of shaft, second trochlea not preserved, other trochlea pitted, no distal foramen, juvenile; AM MF771, distal. Quaternaty.

Wombeyan Quarry, New South Wales — Tib., AM P58025, distal end and distal one-third of shaft. Tint., AM P58026, proximal. Late Pleistocene.

#### Comments and Description

Dromaius novaehollandiae is the only extant species. A number of subspecies have been suggested (Condon 1975), but little is known of their ranges or morphological distinctness. The osteological characteristics of the species have been described above. There is a suggestion that a slightly smaller, as well as a larger form of Dromaius novaehollandiae existed during the Pleistocene. The name gracilipes proposed by De Vis for the smaller form was applied to a juvenile D. novaehollandiae (see below). Hence the smaller form; if real, is yet unnamed. As the evidence is limited, we have chosen not to create a separate specific or subspecific names. De Vis also described a larger species of emu, D. patriclus, which we have also synonymized with D. novaehollandiae (see below).

### Dromaius patricius (De Vis)

### Lectotype (here designated)

QM F5547, proximal right tibiotarsus, King Creek, Darling Downs, south-eastern Queensland, Pleistocene.

# Measurements

Tables 9 and 11,

# Referred Material

De Vis assigned a coracoid, and a proximal and a distal tibiotarsus to this species without naming a type specimen. The left coracoid, QM F1120, was only provisionally referred to *patriculs* (De Vis 1888; 1291). In actual fact it is not even a bird bone. The bone is not hollow, and it projects too far lateral to the point taken by De Vis for the glenold facer to conform with an emu coracoid, Additionally, it lacks a pneumatic foramen. It is too large, heavy, and robust to match any bird. It is probably part of a mammalian pelvis.

The distal end of the left (not right as De Vis states) tibiotarsus, QM F5548, which De Vis assigned to D. patricius is not distinguishable from D, novaehollundiae. De Vis also stated (p. 1290) that: 'the rotular surface is relatively longer fore and all to a considerable extent and less concave transversely', but he admitted (p. 1291) that this: 'is perhaps in some measure due to abrasion'. The difference in the 'eminences and ridges for muscle insertions' anteriorly are also as De Vis states (p. 1291): 'scarcely of specific value'. This specimen is within the size range of D. novaehollandiae:

Hence we designate the proximal right tiblotursus, QM F5547, as the lectotype of Dmmanus patricius. It is in most respects trivially different, if at all from D. novaehollandiae. The proximal width for the articular surface) is greater than any 12 novaehollandiae in our sample (\$7.6 mm vs a maximum of SS.6 mm for novaehollandiae, sample size, n=9). The inner cnemial crest (>90.2 mm) is unfortunately not entirely preserved. It may have exceeded the maximum of our sample of D. novaehollandlae (103.1 mm), Concerning other points raised by De Yls, the fibular crest does not altach more proximally, but the bone is thicker at the most proximal point of this crest, the external cnemial crest does descend more distally and a groove between the external and internal cnemial crests does exist that is larger than is present in D. novnehollandlae. We feel that the variability exhibited by D. patricitis would not fall outside that of a large sample of the living emu,

De Vis (1905) also referred a synsacral fragment (consisting of the neural canal of several synsacral vertebrae), QM E5549, to *D*, *patricius*, though it is so incomplete as to render diagnosis difficult. It is within the size range of *D. novaehollandiae* and probably could be referred to that species. We have, however, chosen to assign it only to Casuariidae indeterminate. It was collected from Wurdulumankula, a Cooper Creek locality.

De Vis (1892) referred a part of a distal end of a femur (likely to be QM F1143, in part), the proximal third of a tarsometatatsus (likely QM F1121), the 'calcaneal region of another metatarse' (apparently lost subsequently) and a distal tarsometatarsus (likely QM FI143 in part) lo D. patricius. As De Vis did not figure or describe these specimens in any detail, we are assuming that the OM specimens listed are those referred to in his 1892 paper. They agree with the (limited) description, were collected in the Datling Downs according to the museum labels accompanying the specimens, and appear to bear (on the fossils themselves) De Vis' handwriting. Of these, only the distal tarsometatarsus is described. It is stated to be larger in almost all of its dimensions than the living Emu. It is, indeed, wider than any in our small sample both in the shaft and in its Irochlear expansion, and trochlea 3 is deeper than those in our sample of D. novachollandiae. The proximal tarsometatarsus is very worn; it lacks both the internal and external cotyla, the intercotylar region, and the hypotarsus. It is within the size range of the living D, novaehollandiae. The femur is also very fragmentary; only the popliteal region is preserved, and it, too, lies within the range of D. novaehollandiae.

Etheridge (1889) referred a distal right tibiotarsus, MM F12074 (and cast AM L516) to *D. patricins*, but contrary to his assertion, the specimen is not larger than nor of a different shape to that element in the modern emu. It should be referred to *D.* novaehollandiae.

Thus, some of the specimens that have been considered to be *D. patricius* are indistinguishable from *D. novaehollandiae*. Others may be slightly larger in some measurements, but we doubt that *D. patricius* deserves, on that account, specific status, because our sample of the living emu is still small. We, therefore, synonymize *D. patricius* with *D. navaehollandiae*.

# Dromaius gracilipes (De Vis)

#### Holotype

Tint. QM F1142, Darling Downs, Queensland, Pleistocene.

#### Measurements

Tables 10 and 11.

### Description

De Vis based this species on a distal left tarsometatarsus, QM F1142, with the second and fourth trochleae not preserved and the margins of the third trochlea very eroded. The characteristics which De Vis used to distinguish this from D. novaehollandiae are the lack of a distal foramen and associated muscle cunal, inferior size of the distal end, antero-posterior compression of the shaft, and disproportionate size of the mesial trochlea. These are all juvenile characteristics. De Vis also states that the width of the third trochlea taken from centre of the lateral depressions (i.e. the ligamental pits) is greater in D. gracilipes than in D. novaehollandiae. This is not the case. We therefore synonymize D. gracilipes with D. novaehollandiae.

## Metapterya bifrons (De Vis)

### Type

Tint. QM F1135, locality not given, but presumably Darling Downs, Queensland, Pleistocene.

### Measurements

Table 11.

### Description

De Vis erected this genus and species on the basis of a left distal tarsometatarsus, QM F1135, and allied it with the kiwis because: the trochlea appear to be borne on the ends of moderately long stalks' (De Vis 1892: 449), the lateral trochlear processes (i.e. the second and fourth trochleae) are almost equal in length, the medial trochlea extends beyond the others, the posterior surface of the shaft shows the lines of junction between the coalesced segments, and it lacks a distal foramen which perforates the shaft. De Vis considered the possibility that these might be invenile characteristics, but unfortunately dismissed this idea. De Vis was of the opinion that the fourth trochlea was shorter (that it was a right tarsometatarsus), but actually the second trochlea is shorter. The comparatively large intertrochlear notches, the rough pitted caps on the trochleae, and the points raised by De Vis (presence of epiphyseal lines, lack of distal foramen) are indications that the specimen is of a juvenile bird. As De Vis himself noted, the fossil does not have any articulation for the hallux possessed by kiwis, and the middle trochlea is too large for that of a kiwi. Metapteryx bifrons in all respects conforms to a juvenile individual of D. novaehollandiae, and we synonymize it with that species

# Dromaius ocypus (Miller)

### Holotype

Tint, SAM P13444, Lawson-Daily Quarry, Lake Palankariana, eastern Lake Eyre Basin, South Australia, Mampuwordn Sands, Palankarinna fauna, Pfiocene.

# Measurements

Tables 8, 9, 10 and 11.

### Referred Material

F. UCMP RASS176, condyles, trochanter, and most of head not preserved. *Th*, UCMP RAS5182, distal. Same locality as type.

# Description

Miller (1963) established this species from an essentially complete, but somewhat distorted and cracked right tarsometatarsus, SAM P13444. The overall length, width across the distal end, depth across the internal cotyla and proximal width are all less than similar measurements in living and fossil *D. novaehollandiae*. Additionally, the curvature of the intercotylar region is more pronounced (convex dorsally) than in *D. novaehollandiae*. As noted by Miller (1963), the trochleae have already attained the size and proportions of *D. novaehollandiae*. The width across the distal end is smaller, in part because the intertrochlear notches are narrower than in *D. novaehollandiae*.

The femur and tibiotarsus are provisionally assigned to *D. ocypus*, although they lie within the range of *D. novaehollandiae* in those parts which are preserved, because they were found in the locality of the type specimen. The tarsometatarsus of *D. ocypus* differs most noticeably from *D. novaehollandiae* in its shortness. Unfortunately, the referred specimens are incomplete, and their length cannot be ascertained.

### Dramalus gidju n. sp.

### Holotype

SAM P26779. Associated left leg elements.

## Type locality

Leaf locality (UCMP V6213), Lake Ngapakaldi, eastern Lake Eyre Basin, South Australia, Wipajirl Fni. Kutjamarpu fauna, Medial Miocene.

### Description

An incomplete left leg, consisting of the distal fragment of the tibiotarsus (originally UCMP 71397), the proximal part of the tarsometatarsus (originally UCMP 71398), and a complete pes (originally UCMP RASS234). The tibiotarsal fragment articulates with the tarsometatarsal fragment. The pes is complete but does not articulate with the tarsometatarsal fragment as the trochleae of the tarsometatarsus are not preserved. All fragments were found in close proximity and the assumption is made here that they are from one individual, Dr R.A. Stirton in his field notes of 19 July 1962 assumed that the leg and foot elements were all from one individual and assigned them a single field number RAS 5234.

### Etymology

From an Aboriginal word meaning 'small' (Anonymous 1965, language not specified).

Measurements

Tables 9, 10 and 12.

Referred material None.

### Diagnosis

A small emu with a slender antero-posteriorly commessed tibiotarsus and tarsometatarsus. The anterior lip of the intercotylar region is convex dorsally in D. gidju (as in D. ocypus compared to nearly flat in D. novaehollandiae). The intercotylar region does not extend far proximal to the articular surface as it does in *Casuarius*, however, The lateral lip of the external cotyla is noticeably convex laterally in D. gidju (weakly so in D. novaehollandiae). The width and depth of the proximal articular surface are much less than in D. ocypus and D. novaehollandiae. The D. gidju tibiotarsus is much smaller than those in our D. novaehollandiae sample, but is similar in general appearance and proportions of the distal end, Anteriorly the tarsometatarsus proximal to the condyles is somewhat crushed. The external ligamental prominence above the external ligamental pit is not as well defined in D. gidju as it is in D, novaehollandiae. The anterior ligamental fossa appears proportionally larger and deeper than in D. novaehollandiae. The phalanges (except the second phalany of the second digit) are smaller than those in D. novaehollandiae. Digit II is comparatively longer relative to the other digits than in D. novaehollandine (64% of the length of digit 111 versus 57.5-60.5% for our sample of D. novnehollandiae (see Tables 2 and 12); the first phalanx of digit It is 85% of the proximal depth of the first phalanx of digit 111 versus 76.5-78% for our sample of 12 novaehollandiae, and 66% of the proximal width of digit 111 yersus 52-53% for our sample of D. novaehollandiae). Digit IV is also comparatively longer but less change has occurred (68% of the length of digit 111 versus 62-64% for our sample of D. novaehollandiae, the first phalanx of digit IV is 78% of the depth of the first phalanx digit III versus 73-75% in our sample of D. novuehollandiae). Excepting the proximal phalanges, the ratio of maximum proximal depth to width is creater in D. gidju: thus, the phalanges of D. noruehollandtue are more dorso-ventrally compressed than in D. gid/u. The ungual phalanx of digit II in D gidju is longer than the ungual of digit III (which is pourly preserved). This is not due to an clongation of the ungual of digit 11 in D. gidju, as in Casuarius, but the weak development of the digit III uneual.

#### Comment

From what is known of its hind limb structure, it would appear that *D. gidju* was less cursorially adapted than *D. novaehollandlae*. This is based on the greater length of digits II and IV relative to digit III in *D. gidju* as compared to *D. novaehollandiae*. This foot structure is presumably adapted for greater maneuverability in forested or less open conditions and greater ability to move over regions of a somewhat unpredictable nature.

# Dromaius sp. indet.

Several specimens because of their fragmentary nature and/or unusual proportions could not be assigned to species level. Other specimens were referrable only to Casuarlidae indet. (see following section).

### Referred Material Tables 3-12

No Locality Data — *Imt.*, AM F58087. distal end, trochleae not preserved.

Alcoota, Northern Territory — Tint., QM QA205, third trochlea only; QM QA505, distal, fourth trochlea not preserved. UCMP RAS5397 (in part), a third trochlea only. Ph., QM QA504, first phälans, third digit; UCMP RAS 5397 (in part), second phalans, second digit. The Alcoota specimens are close to D. gidiu. Late Mlocene.

Baldina Creek? (near Burra), South Australia — *E*, SAM P17103, shaft only, partially reconstituted in plaster. Quaternary,

Cooper Creek, South Australia — Thit., QM F1121, proximal, badly croded articular surface. Could be Pliocene-Recent in age.

Lancefield, Victoria — *Tint.*, NMV P35578, distal shaft, Pleistocene in age, dated at about 26 000 B.P. (Gillespie *et al.* 1978).

Warburton River, South Australia — *Ib.*, QM F6668, distal, condyles not preserved, ('Kalamurina?' is pencilled on the bone). *Thut.*, QM F6671, proximal, incomplete fusion of metatarsals dorsally, farsal cap not preserved, juvenile. Pleistocene-Recent in age.

Wellington Caves, New South Wales — St., AM F25218, figured (Anderson, 1934), incomplete. Thu, AM 'A' distal, trochleae not preserved; AM F10850 (cf. D. novaehollandiae), proximal end plus proximal part of shall, articular surface ended. Pleistocene.

#### Dramallnar indet.

Referred Material Tables 3-12.

No Location Data — Syn., QM 16673, fragment, fused vertebrae only.

Bingara, New South Wales — Syn., MM F16795, fused vertebrae only. Pleistocene.

Conper Creek, South Australia — E., HM B776, dorsal vertebra, 24th-26th?, centrum and left postzygapophysis only, (Lower Cooper, locality 2). E., HM B777, part of a left internal condyle and internal popliteal fossa region only; UCMP 60532, popliteal fossa region only, (Karipiri Waterhole, UCMP site 9, V-5861). The locality suggests all specimens are *Dromaius* sp. Pleislocene.

Lake Kanunka, South Australia — K r. UCMP 60560, third or fourth vertebrae?, proximal (dorsal) only, (Site L. UCMP V-5772). Probably *Dromalus*; other *Dromalus* elements known here. Probably Late Pliocene, possibly Pleistocene.

Lake Kittakittaooloo, South Australia — 7mL, SIAM 75, fourth trochlea only, pitted, juvenile. Late Pliocene, possibly Pleistocene.

McEachern's Cave, Victoria — V. r. NMV P157354, dorsal fragment: NMV P157358, dorsal fragment; NMV P157362, dorsal fragment; NMV P157366, dorsal fragment, one facet not preserved, Probably *Dromaius*. Quaternary,

Naracuorte, South Australia — V. r. SAM P18107, third vertebrae?, dorsal fragment, (Henschke's Bone Dig); SAM P18251, dorsal fragment only but facets not preserved, (Henschke's Bone Dig); SAM P18784, third vertebrae?, dorsal fragment (Henschke's Bone Dig); SAM P22812 (in part), third or fourth vertebrae?, dorsal fragment. The locality suggests these specimens are *Dromulus*. Quaternary, probably Late Pleistocene.

Warburton River, South Australia — Syn., UCMP 56647, acetabulum and pectineal process only. Quaternary.

Wombeyan Quarry, New South Wales - Tih., AM P58027, cf. Dromaius, distal end. Late Pleistocene.

# Aves indet.

(previously assigned to Dromants)

Referred Material Tables 10 and 11.

Kalamurina, South Australia — Thr., SAM P11552, distal end, second trochlea not preserved, large. Perhaps Dromornithidae (Table 11). Quaternary.

No Locality Data — 77b., SAM P17148, proximal shaft only; articular surface and enemial crests not preserved. Possibly not avian — the bone is rather dense.

Dromaius ater and D. baudinianus are not reviewed here as Parker (1984) has recently revised their taxonomy.

### DISCUSSION

At least one species of emu, D. gidiu, was present in central Australia in the mid-Miocene. It is known from the Lake Ngapakaldi in northern South Australia and associated with the Kutjamarpu fauna. It does not differ sufficiently from other emus to require crection of a new genus. While the intercotylar region of the fossil tarsometatarsus resembles the condition found in Casuarius in that is is not markedly flattened as in the llying Dromanus, this character state is also true of D. ocypus, an undoubted emu from the Plincene. The shape of the margin of the internal cotyla of the fossil is similar to that of Dromaius and dissimilar to that of Casuarius, which is more excavated posteriorly. The posterior surface of the tarsometatarsus of D. gidju is unfortunately chipped and cracked, but the shape of the remaining fragment of the hypotarsus and tarsal cap appears more cmu-like than cassowary-like. Comparing the pes of the Miocene fossil with recent emus it is obvious that the foot structure has undergone change through the last few million years. The second and, to a lesser extent, the fourth toes have undergone a reduction in size. This trend is parallel with several other ratites (the ostrich and some of the Dromornithldae; Rich 1979), and would appear to be a cursorial adaptation similar to the reduction and eventual loss of lateral and medial digits within horses (Equidae). The pes of D. gigin is more cassowary-like than that of any known living or other fossil enus, implying that in the Miocene, emus were not as highly adapted to an open plains. cursorial lifestyle as they are now. The pes does not, however, contain the specialized ungual spike on digit 11, which so characterizes the cassowaries, D. gigiu appears to be a species that may be close to forms which gave rise to both emus and cassowarles. Based on material now available. D. gidiu has a few specialized characteristics that seem to ally it with Dromaius. But, as our records of this form increase, there may be sufficient reason to separate it from both genera within this family as an early, quite unspecialized form.

A small emu of Miocene age, is also known from Riversleigh, Queensland. This material is currently under study by Walter Boles (Australian Museum). By Late Miocene or Early Pliocene times a species near in size to D,  $gld/\mu$  is known in the Alcoota fauna. It is represented by tarsometatarsal and pedal fragments. This form may be referrable to D,  $gld/\mu$ . The two phalanges differ slightly from those of the Lake Ngapakaldi form, which we have referred to D:  $gld/\mu$ , but are within the range expected for intraspecific variation. Until more complete material is available from Alcoota, however, assignment to Dromalus sp. indet, is preferable. It is certainly not referrable to Casuarius, as the second trochlea is much more reduced relative to the other trochleae, similar to the condition in Dromaius.

By mid-Plicence, a second species of emu, D. ocypus Miller, intermediate in size between D. gidju and D. novaehollandiae, existed. It is known from a right tarsometatarsus and part of a femur and thiotarsus. The femur and thiotarsus are, in those parts which are preserved, not unlike D. novaehollandiae, but if complete would probably be shorter than the corresponding elements in D. novaehollandiae.

In any event, D. novaehollandiae existed by the Late Pliocene or Early Pleistocene. Since then only D. novaehollandiae has been present on the mainland. It has probably fluctuated slightly in size, presumably as a result of a host of selection pressures such as elimate (both temperature and rainfall), diet, predation pressure and competition.

The species restricted in Recent times to King Island and now extinct may possibly extend into the Pleistocene. Localities on King Island are as yet not carefully dated. The emus of King Island (D. minor) and Kangaroo Island (D, baudinianus) appear to be separate species (Parker 1984), The populations on both of these are most likely relics isolated by rising sea levels at the end of the last glaciation of a population that perhaps was once more widespread. Other than their smaller size the King and Kangaroo Island emus differ but little from the mainland emu. The main osteological difference is in the shape of the skull (Spencer & Kershaw 1910, Morgan & Sutton 1928). Possibly also the distal foramen of the tarsometatarsus differs (Shane Parker pers, comm.), but there is considerable variability in this character in the mainland emu. The degree to which the groove, for the musculus adductor digiti IV is roofed over by bone would appear to be age related. In juvenile emus the arch is almost completely lacking, whereas in some adult specimens it is completely formed in bone. Thus, this character is not taxonomically significant for emus, Some Australian mainland fossil emus are within or just larger than the size range for D, minor tabulated in Rich (1979). At Lake Menindee, two distal tibiotarsi (UCMP 53825, includes RHT6 and RHT25) lie within the range of D. minor for the width across the condyles and depth of external condyle but exceed D, minor in the depth of the internal condyle - both specimens measure 37.0 mm in depth of the internal condyle; the range of a sample of 50 D. minor was 26.2-36.1 mm, the mean was 30.4 (Rich 1979, Table 33). What the relationship of these fossils is to D. minor is unresolved and will remain so until a much larger tossil sample of mainland birds is at hand.

De Vis (1892) did describe a smaller mainland

Pleistocene species, D. gracilipes, but hls type specimen is undoubtedly an immature D. novae hollandiae. Nevertheless, smaller emus did exist in Australia In the Pleistocene. Of specimens listed in the systematics section (above) the following lie below the range for modern emus in one or more measurements: AM — unregistered tarsometatarsus, 'A', F10949, MF771; HM B775/869; QM F1121; SAM — P13118, P18099; UCMP — 53825, 53832, 55983, 60532, 79510, RHT1064.

The presently known fossils of mainland emus smaller than the living *D. novaehollandiae* are unfortunately few. We do not believe that they are representatives of *D. minor* or *D. haudinianus*, because of the age of the fossils on the islands is Late Quaternary. We favour the idea that speciation on King and Kangaroo Island could have taken place in very little time geologically speaking. Strong selection for dwarfism quite likely occurred after these emus became isolated at the beginning of the last interglactal (i.e. the Holocene).

The mainland emu, D. novaehollandiae, may have been at any one time in the Pleistocene both larger or smaller than at present. However, there is a possibility that the differences seen in fossil samples are more apparent than real, since the sample size of modern emus is still fairly small and some of the emus in osteological collections were recovered from zoological gardens. Whether or not estant wild emu populations differed significantly in size is largely unknown. As our sample did not contain representatives from the Northern Territory or Western Australia, it is also unavoidably biased geographically.

Periodic dwarfing of the mainland form may have been caused by the same selective agents which produced dwarfing in the island forms. We were unable to test the hypothesis that size changes were related to palaeoclimate or other environmental variables because there are too few reliably dated emit specimens in the Quaternary collections.

De Vis recognized D: patrieius as a separate, larger species of emu, but we can see no significant size difference from D novaehollandiae, Perhaps D. patrichus differed in its proportions from D novaehollandiae. As so few complete bones are known, however, this is difficult to assess. For example, a tibiotarsus SIAM 61 was found to have a smaller length to distal width ratio than most modern emus, but this difference did not prove statistically significant (p > 0.05, t-test).

There was a mass extinction of the Australian megafauna [the larger macropodids, diprotodontids, dromornithids, etc. just before the Holocene (Tedford 1967, Gillespie *et al.* 1978)] suggesting a widely acting selective agent against large size.

There is a suggestion that the Tasmanian cmu,

D. diemenensis, averaged slightly smaller than the mainland form. This idea stemmed from the known eggs of the Tasmanian emu measuring slightly smaller than those of the mainland emu (Dove 1926), and from the recollections of Legge (1907). who saw the Tasmanian emu as a boy. On the other hand, Spencer & Kershaw (1910) report that the Rev. Knopwood captured an 'Emew 60 lbs, weight' on 9 October 1804 in Tasmania, Scott (1924) gives the dimensions of a leg of the Ilusmanian emu collected by Gunn in the 19th century; it is as large as those of the mainland. The fossils of the Tasmanian emu are large (Scott, 1924, 1932) indicating that the larger Pleistocene form of the mainland also reached Tasmania, presumably at a time when Bass Strait did not exist - during a glacial period of lowered sealevel. Concerning the extinct Recent Tasmanian emu, the best evidence supports the view that it was about the same size as the mainland emu. Condon (1975), following Ridpath & Moreau (1966), treated the Tasmanian emu as a subspecies of D. novaehollandiae. Kathryn Medlock (Tasmanian Museum) is currently reviewing the status of this form.

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TABLE 2. Statistical summaries of the extant emu *Dromaius novaehollandiae* ( $\bar{x}$ , mean; s, standard deviation; n, sample size).

	Range (mm)	x	S	n
Skull				
Length	140 -165	154	6.3	16
Width	58.7- 76.5	68.4	4.1	21
Depth	44.7- 50.7	48.0	1.6	19
Diameter of Foramen Magnum	9.3-13.1	11.0	1.0	25
Length of Lower Jaw	131 -155	145	6.5	21
Symphysial Length of Lower Jaw	16.4- 23.0	21.0	2.4	23
Sternum				
Maximum Length	114 -164	143	11.4	25
Maximum Width	104 -141	125	8.2	25
Number of Costal Processes	3 - 5	4	0.49	28
Width of First Costal Process	98.7-134	116	8.2	24
Width of Last Costal Process	76.4-112 5	96.8	8.2	24
Length of Costal Margin	42.4- 66.9	56.0	7.2	24
Length of Sternocoracoidal Process		33.3		
Width of Coracoidal Sulci	16.3-44.7		8.2	24
	40.2- 62.2	51.9	5.9	24
Anterior Depth	14.4- 20.4	16.7	2.0	23
<i>Scapulocoracoid</i> Proximal Width	100 65 6	45.0	4.0	
	38.9- 55.6	45.9	4.9	20
Maximum Length	151 -187	168	11.3	18
Scapular Length	98.4-127	114	8.7	18
Minimum Width of Coracoid	13.1-22.0	16.I	2.2	20
Minimum Width of Scapula	5.9- 8.9	7.3	1.0	19
Clavicles				
Length	35.2- 53.3	44.0	5.1	12
Maximum Width	3.6- 8.1	5.5	1.2	12
Depth	2.0- 4.9	3.4	0.8	12
Humerus	0.0 1 0.0 4			
Length	83.1-98.7	90.3	4.2	20
Proximal Width	5.4- 8.3	6.4	0.8	20
Proximal Depth	6.2- 7.9	6.9	0.5	20
Ulna				
Length	57.5-73.0	64.9	4.5	20
Proximal Width	3.6- 4.8	4.2	0.3	20
Proximal Depth	3.3- 4.8	4.0	0.4	20
Radius	<i></i>	12.1		
Length	55.2- 68.9	63.1	4.1	20
<i>Carpometacarpus</i> Length	36 6 60 6	13 6	3.4	
Proximal Width	36.6-50.6	43.6	3.6	20
	7.7-12.3	10.0	1.2	20
Proximal Depth	4.6- 6.5	5.5	0.5	20
Distal Depth	2.5- 4.4	3.4	0.5	19
Manus Bl. Lougth	10.0 02.2	19.4	4.4	4.0
Pl, Length	10.0- 26.6	13.6	4.1	13
P1, Proximal Diameter	4.2- 6.9	5.0	0.8	11
P2, Length	4.8- 8.0	6.3	1.4	5
P2, Proximal Diameter	1.9- 3.7	3.0	0.7	- 5
P3, Length	6.1-14.9	10.4	2.7	6
P3, Proximal Diameter	14.0- 5.2	2.8	1.3	6

	Range (mm)	x	S	n
Synsacrum				
Length	337 -412	378	24.7	17
Diameter of Acetabular Foramen	12.3- 21.0	17.3	2.3	23
Width across Antitrochanter	90.9-109	101	5.3	22
Maximum Depth	88.7-109.2	99.3	4.2	23
Femur			40.4	
Length	175 -218	203	10.1	22
Proximal Width	62.0- 68.0	64.9	2.0	10
Proximal Depth (Trochanter)	55.8- 63.4	59.7	2.5	10
Diameter of Head	23.5-29.7	26.4	1.5	26
Distal Width	65.4-79.2	71.7	3.2	26
Depth of External Condyle	64.0- 75.4	69.3	2.9	26
Tibiotarsus	240 422	401	21.8	18
Length	340 -432 19.5- 27.0		1.8	23
Diameter of Shaft, Minimum		23.1 28.1	2.2	23
Diameter of Shaft, Maximum	24.6- 34.2 86.2-103	28.1 96.2	5.6	23 9
Proximal Depth	47.4- 55.6	52.4	2.8	9
Proximal Width	74.6-110	90.4	12.1	9
Length of Fibular Crest	38.7-47.4	42.7	2.8	9
Depth, Internal Condyle	36.5 - 47.4 36.5 - 45.9	42.7	2.0	26
Depth, External Condyle Width, Distal End	38.9 - 49.1	41.0	2.2	25
	5017 1714	1017		
<i>Fibula</i> Length	231 -305	272	20.9	12
Proximal Width	13.9- 19.0	17.1	1.5	22
Proximal Depth	35.2- 48.7	38.7	3.0	22
Tarsometatarsus				
Length	332 -422	383	18.0	22
Minimum Diameter of Shaft	11.6- 17.3	14.7	1.5	23
Maximum Diameter of Shaft	16.8- 23.1	19.9	1.5	23
Proximal Width	47.2- 54.0	50.0	2.1	25
Depth of Internal Cotyla	25.4-27.6	26.6	0.8	9
Depth of External Cotyla	19.9-23.7	22.0	1.2	9
Depth of Hypotarsus	36.0- 41.3	38.5	1.7	8
Distal Width	47.4- 54.6	51.1	2.0	8
Tarsometatarsus, trochleae				
Width T2	9.0-11.1	10.0	0.8	9
Width T3	21.9-28.9	24.9	2.0	24
Width T4	12.2- 14.9	13.6	1.0	9
Depth T2	13.0- 17.6	15.4	1.4	9
Depth T3	19.0- 24.3	22.2	1.8	9
Depth T4	14.3- 17.2	15.6	1.0	9
Pes	40.7 53.9	47 4	20	1.
DII P1 Length	40.7-52.8	47.4	2.8 1.7	14
Proximal Depth	16.3 - 21.4 13.2 - 16.4	18.5 14.8	0.8	1.
Proximal Width	17.1- 22.4	19.5	2.1	13
DII P2 Length Proximal Depth	11.6- 13.3	12.3	0.6	13
Proximal Width	12.4- 15.6	14.0	1.0	13
	21.4- 28.2	25.9	2.2	9
DII P3 Length Proximal Depth	9.4- 12.2	11.0	0.8	10
Proximal Depth Proximal Width	10.4- 12.9	11.5	0.9	10
DIII P1 Length	58.1- 65.7	60.5	1.9	14
Proximal Depth	21.3- 27.3	23.6	1.5	14
Proximal Width	25.3-31.1	27.5	2.0	1.
DIII P2 Length	33.4- 42.8	38.8	2.3	13
Proximal Depth	15.0- 18.9	16.9	0.9	1.
Proximal Width	20.3- 25.4	22.5	1.6	14
I I OAIIIIIII II IUIII	20.J. 20.T	an an 1 - J	1.0	

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	Range (mm)	x	S	1
DIII P3 Length	19.5 - 29.3	23.6	2.8	1
Proximal Depth	12.1-14.1	13.1	0.7	1
Proximal Width	17.2-20.8	19.0	0.9	1.
DIII P4 Length	26.7- 34.4	30.4	2.1	4
Proximal Depth	11.7- 14.9	12.9	1.0	1
Proximal Width	14.8- 17.7	15.6	0.9	1
DIV P1 Length	33.7- 41.2	38.5	2.0	1
Proximal Depth	16.0- 19.8	17.3	0.8	1:
Proximal Width	16.0- 19.2	18.0	0.8	1:
DIV P2 Length Proximal Depth	14.9- 18.2 11.1- 13.2	17.0	1.0	1
Proximal Width	14.2 - 16.0	12.5 15.1	0.6	1
DIV P3 Length	14.2 - 10.0 10.5 - 14.4	12.0	0.5	1
Proximal Depth	9.9 - 12.1	12.0	0.6	1
Proximal Width	12.5- 14.9	13.2	0.6	1
DIV P4 Length	6.4- 12.3	9.7	1.6	1
Proximal Depth	8.7-10.7	10.1	0.6	1
Proximal Width	10.4-13.4	12.0	0.8	1
DIV P5 Length	19.2- 24.3	22.2	1.6	1
Proximal Depth	9.3- 11.8	10.5	0.7	1
Proximal Width	10.1-11.5	10.9	0.5	1
Vertebrae			010	
C1 Length, Ventral	5.0- 7.9	6.1	0.8	1
Depth of Hypopophysis	5.3- 6.1	5.8	0.3	1
Maximum Width across Arch	12.8- 16.5	14.5	1.4	
Depth	14.9- 17.7	16.1	0.8	I
Prearticular Surface	6.2- 8,5	7.1	0.7	1
Postarticular Surface	9.0- 11.3	10.4	0.8	i
Dorsal Length	5.8- 7.3	6.4	0,5	1
C2 Depth	25.7- 30.9	28.1	1.4	1
Width across Postzygapophyses	20.4-24.9	22.3	1,3	1
Width across Diapophyses	12.2- 15.5	13.8	1.0	1
Width across Postarticular surface	6.3- 8.7	7.3	0.7	1
Width across Prearticular surface	9.7-11.4	10.5	0.5	1
Centrum Length	15.9-20.5	18.3	1.5	1
Length from Pre- to Post Zygapophyses	14.1-17.9	16.6	1.1	11
C3 Depth	21.0- 26.1	23.7	1.3	1
Postzygapophyses	22.7- 28.2	25.4	1.4	1
Diapophyses	17.7-23.5	21.0	1.4	1
Postarticular Surface	6.9- 9.6	8.4	0.7	1
Prearticular Surface	8.1-10.9	9.1	0.8	1
Centrum length	16.5-21.2	18.9	1.4	1
Pre-postzygapophyses	22.3- 27.8	29.8	1.7	1
C4 Depth	18.1-22.6	20.2	1.3	1
Postzygapophyses	22.1-26.4	24.5	1.3	1
Diapophyses	21.6~ 26.8	23.6	1.3	1
Postarticular Surface	9.5-13.0	11.3	1.2	1
Prearticular Surface	7.9- 12.0	10.3	0.9	1
Centrum Length	20.5- 25.3	22.7	1.6	1
Pre-postzygapophyses	26.4- 32.3	29.4	1.9	1
25 Depth	14.9- 19.3	17.1	1.2	1
Postzygapophyses	12.8-19.5	17.0	1.6	1
Diapophyses	25.0- 28.6	26.2	1.1	1
Postarticular Surface	13.6-19.7	16.0	1.6	1
Prearticular Surface	10.5-15.7	13.3	1.6	1
Centrum Length	22.4- 26.7	25.2	1.3	1
Pre-postzygapophyses	30.8- 40.6	36.0	2.5	17
C6 Depth	13.9- 19.7	16.5	1.3	13

	Range (mm)	x	s	n
Diapophyses	$17.4 - 31.1 \\ 16.8 - 20.6 \\ 14.5 - 19.9 \\ 25.3 - 29.4 \\ 25.3 - 29.4 \\ 34.5 - 10.9 \\ 35.5 - 29.4 \\ $	27.8	3.1	17
Postarticular Surface		18.7	1.3	17
Prearticular Surface		17.4	1.7	17
Centrum Length		27.8	1.3	17
Pre-postzygapophyses	35.7- 42.2	38.8	1.8	17
C7 Depth	15.0- 19.0	16.9	1.2	17
Postzygapophyses	11.5- 17.9	14,0	1.8	17
Diapophyses	27.8- 32.9	30.4	1.7	17
Postarticular Surface	15.2- 20.1	18.0	1.6	17
Prearticular Surface	18.9- 24.1	21.0	1.4	17
Centrum Length	28.5- 32.3	30.7	1.3	17
Pre-postzygapophyses	35.7- 41.4	38.4	1.5	17
C8 Depth	16.2- 19.9	18.0	1,1	17
Postzygapophyses	12.1- 19.7	16.8	2.2	17
Diapophyses	18.4- 34.2	30.4	3.6	17
Postarticular Surface	14.4- 19.1	16.9	1.4	17
Prearticular Surface	16.8- 32.2	20.8	3.5	17
Centrum Length	23.6- 35.6	32.9	2.8	17
Pre-postzygapophyses	36.5- 40.5	38.6	1.3	17
C9 Depth	18.2-22.7 $16.3-25.0$ $28.4-34.5$ $13.4-17.9$ $16.1-21.7$ $34.2-38.7$ $38.2-45.3$	20.2	1.2	17
Postzygapophyses		20.8	2.0	17
Diapophyses		31.2	1.8	17
Postarticular Surface		15.4	1.3	17
Prearticular Surface		19.0	1.4	17
Centrum Length		36.2	1.4	17
Pre-postzygapophyses		40.4	1.9	17
C10 Depth	19.7-23.6 $19.8-27.2$ $28.8-34.7$ $12.6-16.7$ $15.2-21.1$ $36.0-40.8$ $40.5-50.6$	21.7	1.2	17
Postzygapophyses		22.9	1.6	17
Diapophyses		31.0	1.8	17
Postarticular Surface		14.8	1.2	17
Prearticular Surface		17.5	1.7	17
Centrum Length		38.4	1.6	17
Pre-postzygapophyses		44.2	2.3	17
C11 Depth Postzygapophyses Diapophyses Postarticular Surface Centrum Length Pre-postzygapophyses Prearticular Surface	21.0- 24.9 21.2- 27.5 29.4- 34.7 13.8- 18.4 37.7- 43.2 43.6- 53.2 15.1- 19.9	23.2 23.4 31.5 15.4 40.7 47.3 16.9	1.2 1.5 1.6 1.4 1.7 2.2 1.6	17 17 17 17 17 17
C12 Depth Postzygapophyses Diapophyses Postarticular Surface Prearticular Surface Centrum Length Pre-postzygapophyses	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	24.6 23.8 25.0 16.5 17.9 42.4 49.7	1.3 1.7 1.5 2.3 1.5 2.3	17 17 17 17 17 17
C13 Depth Postzygapophyses Diapophyses Postarticular Surface Prearticular Surface Centrum Length Pre-postzygapophyses	23.3- 28.2 20.3- 27.0 30.7- 37.3 16.2- 20.6 15.5- 22.6 40.4- 45.9 47.7- 54.4	25.7 23.8 33.7 17.8 18.9 43.6 51.9	1.5 1.9 1.7 1.4 1.9 1.6 1.9	17 17 17 17 17 17
C14 Depth	24.3- 29.7	26.9	1.5	17
Postzygapophyses	20.7- 26.4	23.9	1.7	17
Diapophyses	32.0- 38.5	35.2	1.6	17
Postarticular Surface	17.3- 22.2	19.2	1.4	17
Prearticular Surface	17.1- 23.4	20.4	1.9	17

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	Range (mm)	x	s	n
Centrum length	41.0- 46.5	44.3	1.7	17
Pre-postzygapophyses	48.6- 56.6	52.8	2.3	17
C15 Depth Postzygapophyses Diapophyses Postarticular Surface Prearticular Surface Centrum Length Pre-postzygapophyses	25.6- 32.2 21.4- 27.4 34.5- 40.9 19.0- 23.5 17.6- 25.9 41.2- 47.4 49.8- 58.4	28.6 24.1 37.1 21.2 22.0 44.9 53.6	2.0 1.6 2.0 1.4 2.1 1.8 2.5	17 17 17 17 17 17
C16 Depth Postzygapophyses Diapophyses Postarticular Surface Prearticular Surface Centrum Length Pre-postzygapophyses	27.5- 33.5 22.4- 28.1 36.9- 45.7 20.5- 25.7 20.4- 29.2 41.9- 48.5 51.1- 60.8	30.5 25.4 40.7 23.3 24.1 45.3 55.0	2.1 1.7 2.6 1.6 2.2 1.9 2.8	16 16 16 16 16 16
C17 Depth Postzygapophyses Diapophyses Postarticular Surface Prearticular Surface Centrum Length Pre-postzygapophyses	29.3- 41.1 25.1- 30.4 41.8- 51.4 20.9- 27.6 23.5- 32.4 42.5- 48.7 50.0- 61.2	33.8 27.2 45.7 24.5 26.5 45.5 55.6	3.2 1.9 3.2 1.9 2.2 2.0 2.8	17 17 17 17 17 17
C or V18 Depth Postzygapophyses Diapophyses Postarticular Surface Prearticular Surface Centrum Length Pre-postzygapophyses	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	41.2 28.4 53.6 25.3 27.6 45.1 55.4	5.5 2.0 5.7 1.8 2.6 1.8 3.0	16 16 16 16 16 16
V19 Depth	43.0- 66.4	50.7	6.3	17
Postzygapophyses	25.2- 31.3	28.3	1.7	17
Diapophyses	56.5- 70.6	61.7	4.0	17
Postarticular Surface	21.6- 27.8	24.9	1.8	17
Prearticular Surface	23.4- 33.1	27.4	2.5	17
Centrum Length	40.9- 47.5	44.4	1.9	17
Pre-postzygapophyses	51.4- 58.4	54.2	3.1	17
V20 Depth	50.7- 77.1	62.6	5.7	17
Postzygapophyses	23.7- 30.2	26.5	1.9	17
Diapophyses	62.1- 81.8	67.5	4.6	17
Postarticular Surface	20.5- 25.6	23.3	1.5	17
Prearticular Surface	23.7- 34.0	27.6	2.7	17
Centrum Length	40.4- 47.6	42.8	1.8	17
Pre-postzygapophyses	49.7- 58.3	54.2	2.4	17
V21 Depth	56.6- 78.1	68.0	5.5	17
Postzygapophyses	23.4- 29.1	26.2	1.6	17
Diapophyses	61.3- 82.0	68.2	4.8	17
Postarticular Surface	19.6- 26.5	22.7	1.5	17
Prearticular Surface	21.4- 29.4	25.3	2.0	17
Centrum Length	37.2- 46.3	42.1	2.4	17
Pre-postzygapophyses	47.9- 57.0	51.9	2.7	17
V22 Depth	57.1 - 74.9 $22.4 - 30.5$ $61.0 - 76.8$ $19.8 - 29.1$ $21.9 - 29.1$ $38.3 - 45.5$ $47.2 - 57.8$	64.7	6.1	17
Postzygapophyses		26.7	2.0	17
Diapophyses		67.0	3.7	17
Postarticular Surface		23.3	2.3	17
Prearticular Surface		24.5	1.9	17
Centrum Length		41.5	2.2	17
Pre-postzygapophyses		50.7	2.9	17

	Range (mm)	X	S	n
V23 Depth	55.7- 72.9	63.4	3,3	17
Postzygapophyses	25.8- 33.1	28.2	2.1	17
Diapophyses	60.9- 74.4	67.2	3.9	17
Postarticular Surface	21.0- 26.7	23.7	1.4	17
Prearticular Surface	20.3- 29.0	24.4	2.2	17
Centrum Length	37.8- 43.7	40.4	1.7	17
Pre-postzygapophyses	43.8- 51.6	47.1	2.1	17
V24 Depth	60.2- 79.9	68.7	4.6	17
Postzygapophyses	26.1- 33.8	30.4	2.2	17
Diapophyses	62.1-75.5	68.7	4.I	17
Postarticular Surface	19.8- 28.4	24.3	2.3	16
Prearticular Surface	21.3- 28.8	24.7	2.3	17
Centrum Length	.37.5- 46.1	41.3	2.0	17
Pre-postzygapoplyses	43.2- 52.1	46.9	2.1	17
V25 Depth	63.7- 85.9	74.1	5.2	17
Postzygapophyses	27.9- 40.2	33.8	2.8	17
Diapophyses	43.4- 76.2	68.7	7.7	17
Postarticular Surface	20.3- 27.3	23.8	1.9	17
Prearticular Surface	20.4- 30.3	25.2	2.5	16
Centrum Length	36.8- 44.4	41.2	2.0	17
Pre-postzygapophyses	42.3- 52.9	46.3	2.2	17
V26 Depth	68.5- 87.8	79.4	5.2	15
Postzygapophyses	26.2-40.9	33.7	3.9	16
Diapophyses	59.7-75.6	69.2	4.6	15
Postarticular Surface	23.0- 30.4	25.0	1.9	15
Prearticular Surface	23.1- 38.7	25.8	3.8	15
Centrum Length	33.3- 49.4	40.6	3.6	16
Pre-postzygapophyses	41.2- 50.7	45.3	2.9	15

SPECIMEN	Width	Depth	Diameter, Foramen Magnum	Lower Jaw, Symphysial Length
NMV P157345	75.0 (est.)	47.4	10.8	_
NMV P157350	_	_	— .	21.5
NMV P157353	>65.2	48.5	10.7	_
SAM P17834	—			24.5

SPECIMEN         Depth         Postzyg.         Diapop.         Articulation         Articulation         Centrum         Zygopop.         Number           MM F16786         -         42.2 (est.)         -         25.5 +         30.0 (est.)         37.7         46.3         V24?           MM F16797         -         31.8         -         27.0         27.2         38.8         42.1         V26 or 2           NMV         -         31.8         -         27.0         27.2         39.3         46.3         V21 or 2           NMV         -         23.6         -         20.2         23.2         39.3         46.3         V21 or 2           NMV         -         -         62.8 (est.)         21.4         22.2 (est.)         36.0         -         V23 or 2           NMV         -         -         62.8 (est.)         21.4         22.2 (est.)         31.2         37.8         C11-13?           NMV         -         -         -         11.9         12.4 (est.)         31.2         37.8         C11-13?           NMV         -         -         -         -         -         V25 or 2         V25 or 2           NMV         -			Measurements									
SPECIMENDepthPostzyg.Diapop.Anterior ArticulationAnterior Articulationof Articulationacross CentrumVertebra Zygopop.MM F16786-42.2 (est.)-25.5 +30.0 (est.)37.746.3V24?MM F16797-31.8-27.027.238.842.1V26 or 2NMV-23.6-20.223.239.346.3V21 or 2NMV62.8 (est.)21.422.2 (est.)36.0-V23 or 2NMV14.39.724.616.912.824.530.2C7?NMVNMV14.39.724.616.912.4 (est.)31.237.8C11-13?NMVNMV14.39.724.616.912.4 (est.)31.237.8C11-13?NMVNMV195735218.217.7-11.912.4 (est.)31.237.8C11-13?NMVP15736468.0 (est.)V25 or 2NMVP15736521.4 (est.)26.0 (est.)27.0-V22.26SAM P1876330.527.537.9*20.618.8*48.1-C15-C17SAM P1867330.527.537.9*20.618.8*48.1-C15-C17SAM P1867330.527.537.9*20.618.8*48.1-C15-C17SAM P1867330.5 <t< th=""><th></th><th></th><th></th><th>Widt</th><th>h</th><th></th><th>Lonoth</th><th>Lanath</th><th></th></t<>				Widt	h		Lonoth	Lanath				
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	SPECIMEN	Depth	Postzyg.	Diapop.			of	across	Vertebral Number			
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	MM F16797								V24? V26 or 25?			
NMV         P157351         14.3         9.7         24.6         16.9         12.8         24.5         30.2         C7?           NMV         P157352         18.2         17.7         -         11.9         12.4         (est.)         31.2         37.8         C11-13?           NMV         P157352         18.2         17.7         -         11.9         12.4         (est.)         31.2         37.8         C11-13?           NMV         P157359         22.5         26.1         21.7         8.7         9.2         17.5         24.2         C3           NMV         P157364         -         -         -         -         V25 or 2         NW           P157367         -         19.8         46.8         (est.)         -         -         >36.3         V20-21           NMV         P157368         16.6 <sup>+</sup> 16.6 <sup>+</sup> -         11.0         162         (est.)         29.2         32.4         ?C11           NMV         P157369         -         -         -         -         >36.3         V20-21           SAM P18546         19.9         23.9         22.5         10.7         9.8         23.2	P157346	-	23.6	-	20.2	23.2	39.3	46.3	V21 or 22			
NMV       International and the state of th		-	-	62.8 (est.)	21.4	22.2 (est.)	36.0	-	V23 or 24			
NMV       P157359       22,5       26.1       21.7       8.7       9.2       17.5       24.2       C3         NMV       P157364       -       -       68.0       (est.)       -       -       -       V25 or 2         NMV       P157367       -       19.8       46.8       (est.)       -       -       -       V25 or 2         NMV       P157367       -       19.8       46.8       (est.)       -       -       -       >36.3       V20-21         NMV       P157368       16.6 <sup>+</sup> 16.6 <sup>+</sup> -       11.0       16.2       (est.)       29.2       32.4       ?C11         NMV       P157369       -       -       -       21.4       (est.)       26.0       (est.)       27.0       -       V22-26         SAM P17589       29.7       23.1       39.7       21.8       23.1       47.4       54.0       C16 (15-1         SAM P18246       19.9       23.9       22.5       10.7       9.8       23.2       29.5       C4         SAM P18830       -       33.4       -       27.4       >25.6       39.7       44.0       V26?         SAM P18247 <t< td=""><td></td><td>14.3</td><td>9.7</td><td>24.6</td><td>16.9</td><td>12.8</td><td>24.5</td><td>30.2</td><td>C7? (juv)</td></t<>		14.3	9.7	24.6	16.9	12.8	24.5	30.2	C7? (juv)			
NMV       -       -       68.0       (est.)       -       -       -       V25 or 2         NMV       -       -       68.0       (est.)       -       -       -       V25 or 2         NMV       -       19.8       46.8       (est.)       -       -       -       >36.3       V20-21         NMV       -       19.8       46.8       (est.)       -       -       -       >36.3       V20-21         NMV       -       -       -       21.4       (est.)       29.2       32.4       ?C11         NMV       -       -       -       21.4       (est.)       26.0       (est.)       27.0       -       V22-26         SAM P17589       29.7       23.1       39.7       21.8       23.1       47.4       54.0       C16 (15-1         SAM P18246       19.9       23.9       22.5       10.7       9.8       23.2       29.5       C4         SAM P18673       30.5       27.5       37.9*       20.6       18.8*       48.1       -       C15-C17         SAM P18247       -       -       68.0       (est.)       24.8       41.9       -       V22 or 2:	NMV			-	11.9	12.4 (est.)	31.2	37.8	C11-13? (juv)			
NMV       P157367       P19.8       46.8 (est.)       P1       P10       P157368       P16.6 <sup>+</sup> P11.0       P16.2 (est.)       P29.2       32.4       P11         NMV       P157368       16.6 <sup>+</sup> 16.6 <sup>+</sup> P11.0       16.2 (est.)       29.2       32.4       P11         NMV       P157369       P17       P1.3       39.7       21.8       23.1       47.4       54.0       C16 (15-1)         SAM P17589       29.7       23.1       39.7       21.8       23.1       47.4       54.0       C16 (15-1)         SAM P18246       19.9       23.9       22.5       10.7       9.8       23.2       29.5       C4         SAM P18673       30.5       27.5       37.9 <sup>+</sup> 20.6       18.8 <sup>++</sup> 48.1       C15-C17         SAM P18830       -       33.4       -       27.4       >25.6       39.7       44.0       V26?         SAM P18247       -       -       68.0       (est.)       24.8       41.9       V22 or 22.4         AMNH 9678       24.2 <sup>+</sup> 30.0       (est.)       22.6       11.2       (est.)       22.5 <sup>+</sup> 26.7       C3         AMNH 9678       24.2.4 <sup>+</sup>	NMV	22,5	26.1	21.7	8.7	9.2	17.5	24.2	C3			
NMVP157368 $16.6^+$ $16.6^+$ $ 11.0$ $16.2$ (est.) $29.2$ $32.4$ $?C11$ NMVP157369 $  21.4$ (est.) $26.0$ (est.) $27.0$ $ V22-26$ SAM P17589 $29.7$ $23.1$ $39.7$ $21.8$ $23.1$ $47.4$ $54.0$ $C16$ (15-1SAM P18246 $19.9$ $23.9$ $22.5$ $10.7$ $9.8$ $23.2$ $29.5$ $C4$ SAM P18246 $19.9$ $23.9$ $22.5$ $10.7$ $9.8$ $23.2$ $29.5$ $C4$ SAM P18247 $ 33.4$ $ 27.4$ $>25.6$ $39.7$ $44.0$ $V26?$ SAM P18247 $       C2$ AMNH 9678 $ 26.0$ (est.) $22.0$ (est.) $ 11.2$ (est.) $22.5^+$ $26.7$ $C3$ AMNH 9678 $20.2$ $29.1$ $25.9$ $12.6$ $11.7$ $25.6$ $33.1$ $C4$ AMNH 9678 $19.1$ $16.3$ $34.9$ $23.1$ $23.3$ $35.5$ $45.5$ $C7?$ AMNH 9678 $19.1$ $16.3$ $34.9$ $23.1$ $23.3$ $35.5$ $45.5$ $C7?$ AMNH 9678 $21.7$ $   22.5$ $>37.8$ $48.0$ $C9?$	NMV	-		68.0 (est.)	—	—	-	-	V25 or 26			
NMVP15736921.4(est.)26.0(est.)27.0-V22-26SAM P1758929.723.139.721.823.147.454.0C16 (15-1SAM P1824619.923.922.510.79.823.229.5C4SAM P1867330.527.537.9+20.618.8+48.1-C15-C17SAM P18830-33.4-27.4>25.639.744.0V26?SAM P1824768.0(est.)24.841.9-V22 or 2.3AMNH 967824.2+30.0(est.)22.0(est.)-11.2(est.)22.5+26.7C3AMNH 967824.2+30.0(est.)22.819.532.446.6C6?AMNH 967818.016.832.922.819.532.446.6C6?AMNH 967819.116.334.923.123.335.545.5C7?AMNH 967821.7-36.4-22.5>37.848.0C9?	NMV			46.8 (est.)	-	-	-	>36.3	V20-21 (juv)			
SAM P1758929.723.139.721.820.6(60.7)47.454.0C16 (15-1)SAM P1824619.923.922.510.79.823.229.5C4SAM P1824730.527.537.9*20.618.8*48.1—C15-C17SAM P1824768.0(est.)24.841.9—V22 or 2.AMNH 9678-26.0(est.)22.0(est.)21.822.5*26.7AMNH 967824.2*30.0(est.)22.0(est.)-11.2(est.)22.5*26.7AMNH 967820.229.125.912.611.725.633.1C4AMNH 967818.016.832.922.819.532.446.6C6?AMNH 967819.116.334.923.123.335.545.5C7?AMNH 967821.7-36.4-22.5>37.848.0C9?	NMV	16.6 *	16.6+	-	11.0	16.2 (est.)	29.2	32.4	?C11 (juv)			
SAM P1824619.923.922.510.79.823.229.5C4SAM P1867330.527.537.9+20.6 $18.8+$ $48.1$ —C15-C17SAM P18830—33.4—27.4>25.639.744.0V26?SAM P18247——68.0(est.)24.841.9—V22 or 2:AMNH 9678—26.0(est.)22.0(est.)———C2AMNH 967824.2+30.0(est.)22.0(est.)—11.2(est.)22.5+26.7C3AMNH 9678>20.229.125.912.611.725.633.1C4AMNH 967818.016.832.922.819.532.446.6C6?AMNH 967819.116.334.923.123.335.545.5C7?AMNH 967821.7—36.4—22.5>37.848.0C9?									V22-26 (juv)			
SAM P18673 SAM P18873 $30.5$ $27.5$ $37.9^+$ $20.6$ $18.8^+$ $48.1$ $-$ C15-C17SAM P1830 SAM P18247 AMNH 9678 $ 33.4$ $  27.4$ $>25.6$ $39.7$ $44.0$ $V26?$ SAM P18247 AMNH 9678 AMNH 9678 $  68.0$ (est.) $24.8$ $41.9$ $  V222$ or 2:AMNH 9678 AMNH 9678 $ 26.0$ (est.) $22.0$ (est.) $    C2$ AMNH 9678 									C16 (15-17?)			
SAM P18830 $-$ 33.4 $-$ 27.4>25.639.744.0V26?SAM P18247 $ -$ 68.0(est.)24.841.9 $-$ V22 or 2:AMNH 9678 $-$ 26.0(est.)22.0(est.) $  -$ C2AMNH 967824.2+30.0(est.)22.0(est.) $-$ 11.2(est.)22.5+26.7C3AMNH 9678>20.229.125.912.611.725.633.1C4AMNH 967818.016.832.922.819.532.446.6C6?AMNH 967819.116.334.923.123.335.545.5C7?AMNH 967821.7 $-$ 36.4 $-$ 22.5>37.848.0C9?								29.5				
SAM P18247       -       -       68.0 (est.)       24.8       41.9       -       V22 or 23         AMNH 9678       -       26.0 (est.)       -       -       -       -       C2         AMNH 9678       24.2+       30.0 (est.)       22.0 (est.)       -       11.2 (est.)       22.5+       26.7       C3         AMNH 9678       >20.2       29.1       25.9       12.6       11.7       25.6       33.1       C4         AMNH 9678       18.0       16.8       32.9       22.8       19.5       32.4       46.6       C6?         AMNH 9678       19.1       16.3       34.9       23.1       23.3       35.5       45.5       C7?         AMNH 9678       21.7       -       36.4       -       22.5       >37.8       48.0       C9?												
AMNH 9678       -       26.0 (est.)       -       -       -       -       C2         AMNH 9678       24.2+       30.0 (est.)       22.0 (est.)       -       11.2 (est.)       22.5+       26.7       C3         AMNH 9678       >20.2       29.1       25.9       12.6       11.7       25.6       33.1       C4         AMNH 9678       18.0       16.8       32.9       22.8       19.5       32.4       46.6       C6?         AMNH 9678       19.1       16.3       34.9       23.1       23.3       35.5       45.5       C7?         AMNH 9678       21.7       -       36.4       -       22.5       >37.8       48.0       C9?						>25.6						
AMNH 9678       24.2+       30.0 (est.)       22.0 (est.)       —       11.2 (est.)       22.5+       26.7       C3         AMNH 9678       >20.2       29.1       25.9       12.6       11.7       25.6       33.1       C4         AMNH 9678       18.0       16.8       32.9       22.8       19.5       32.4       46.6       C6?         AMNH 9678       19.1       16.3       34.9       23.1       23.3       35.5       45.5       C7?         AMNH 9678       21.7       —       36.4       —       22.5       >37.8       48.0       C9?												
AMNH 9678       >20.2       29.1       25.9       12.6       11.7       25.6       33.1       C4         AMNH 9678       18.0       16.8       32.9       22.8       19.5       32.4       46.6       C6?         AMNH 9678       19.1       16.3       34.9       23.1       23.3       35.5       45.5       C7?         AMNH 9678       21.7       -       36.4       -       22.5       >37.8       48.0       C9?						11.0 (						
AMNH 9678         18.0         16.8         32.9         22.8         19.5         32.4         46.6         C6?           AMNH 9678         19.1         16.3         34.9         23.1         23.3         35.5         45.5         C7?           AMNH 9678         21.7         -         36.4         -         22.5         >37.8         48.0         C9?												
AMNH 9678         19.1         16.3         34.9         23.1         23.3         35.5         45.5         C7?           AMNH 9678         21.7         -         36.4         -         22.5         >37.8         48.0         C9?												
AMNH 9678 21.7 - 36.4 - 22.5 > 37.8 48.0 C9?												
									V21 or 22 V22 or 23			

TABLE 4. Measurements (in mm) of vertebrae of fossil emus (Dromaiinae) from Australia.

TABLE 5. Measurements (in mm) of vertebral ribs of fossil emus (Dromaiinae) from Australia.

SPECIMEN	Width of Facets
NMV P157354	>36.8
NMV P157358	-34.3
NMV P157362	>28.0
SAM P18107	29.3
SAM P18784	34.1
SAM P22812 (in part)	38.6
UCMP 60560	34.8
	54.0

SPECIMEN	Maximum Length	Maximum Width	Number of Costal Processes	Width of first Costal Process	Width of last Costal Process	Length of Costal Margin	of Sterno- coracoidal		Anterior Depth
D. novaehollandiae NMV P157347		124	3	~118	_	_	_	~52.6	14.6
NMV P157355	_	112	4	109	90.9	49.7	16.4		_
D. sp. AMP 25218	147	118	4	~127	109	64.2	_	70.5	17.9

TABLE 6. Measurements (in mm) of sterna of fossil emus (Dromaiinae) from Australia.

TABLE 7. Measurements (in mm) of synsacra of fossil emus (Dromaiinae) from Australia.

SPECIMEN	Diameter of Acetabular Foramen	Width across Antitrochanter	Length of Acetabular Complex	Depth of Acetabular Complex
D. novaehollandiae				
NMV P157361		>83.6	56.3	
SAM Unreg.	15.5	_		
SAM P16501	18.0	108		—
SAM P17767	12.2	104	60.7	33.8
UCMP 56333	17.4	_	62.3	36.8

TABLE 8. Measurements (in mm) of femora of fossil emus (Dromaiinae) from Australia.

SPECIMEN	Length	Proximal Width	Proximal Depth (Trochanter)	Diameter of Head	Distal Width	Depth of External Condyle
D. novaehollandiae						
HM B775/869	190		600x99999		59.6	61.2 R
HM B801/934		_	_			76.2 d,R
RHT 1064	190	65.1		27.6		— R
SAM Unreg.	_		-	27.4	>76.3	76.7
SAM P17104	_	~67.2	-61.2	-28.0	_	— p,L
SAM P22812	204	67.4	61.4	25.5	68.8	— L
AMNH 9677		_	_	_	83.3	70.7 d,R
D. cf. ocypus UCMP RAS5176	190	59.5	_		_	— p,L

1	1	0	
L	1	U.	
_	_	-	

TABLE 9. Measurements (in mm) of tibiotarsi of fossil emus (Dromaiinae) from Australia.

		Diamete	r of Shaft	Dravimal	Proximal		Depth,	Depth,	Widt	
SPECIMEN	Length	-	Maximum	Depth	Width	Crest	Internal Condyle	Condyle	Dist. Enc	
D. novaehollandiae										
AM 49713		_		113	57,8			-	_	p,R
AM 'B'	_	—			_		45.1		46.6	d,L
AM F10949			_		—		>35.0	31.2	38.1	d,L
AM P5802	-		_	_			41.0	42.1	47.3	d,R
MM F16775				_	_		44.9	44.3	49.5	d,R
NMV P44011		22.1	26.6	>76.0	>44.1	93.1		_		R
NMV P150013		24.9	32.7			95.1	44.7	40.2	50.4	d,I
NMV P157356			_	>92.2	47.4	_			_	p,R
NMV P157357	_		_			<u> </u>	39.1 *		43.3	d,L
NMV P157360							>39.3	39.3	41.8	d,L
NMV P157365		21.1	29.2	>91.5	49.2	96.4		_	_	p,R
QM F1652		_			56.1	>80.5	_		_	p,L
SAM P17149				_			42.7		43.6	d,R
SAM P18829							>38.8	41.3+	>37.5	-
SIAM 61	384	23.3	32.3	102	56.9	88.6	45.8	43.9	51.8	L
UCMP 53825					20.2	0010	1210		21.0	~
(RHT6)	_						37.0	35.1	37.4	41
UCMP 53825							57.0	55.1	27.4	ч,1
(RHT25)	-		_				37.0	34.9	35.6	d I
UCMP 56845	_		_		_			38.8	40.6	
WAM 68.5.34	. <u> </u>	21.6	26.3	_		107			40.0	L,L
						107				-
D. 'patricus'										
MM F12074	_			_			35.5	34.3+	41.3	
QM F5547	—				57.6	>90.2		—		p,R
QM F5548			_				46.2	45.7	48.6	d,L
D. cf. ocypus										
UCMP RAS5182	—		_	_	_		43.0	40.8	46.0	d,R
D. gidju										
SAM P26779	_	_		_			31.8	31.3	32,0	d.I

		Diameter	of Shaft	Proximal	Depth, Internal	Depth, External	Depth,	Dist	al
SPECIMEN	Length	Minimum	Maximum	Width	Cotyla	Cotyla	Hypotarsus	Wid	th
D. novaehollandiae									
AM Unreg.				56.7	25.9	24.5	42.5*		p,R
AM 'C'		_	_	53.9	25.2	21.3	40.5 +	-	p,L
AM F771	-	11.8+	20.5		_		_	47.5	d,R
AM F18935		14.0	19.4	_	-		-	>46.2	d,L (juv)
AM P58026	_	_		53.0	23.2+	19.1+	39.5+	_	p,R
NMV L5		_						54.1*	d,L
NMV P44012		14.1	21.9	>42.3			>34.0	52.4	R
NMV P44013		16.1	22.2	48.3	26.3	22.5 *	>35.1	55.9	R
		14.9	19.8	49.8	24.2	21.4	37.5+	52.2	R
NMV P44014				46.5	24.0+	19.8	>37.0		R
NMV P44015		14.0	19.5						L
NMV P44016	_	15.5	20.4	-united	23.0	>21.8	>38.2	51.2	
NMV P44017		13.3	21.7		_		_	>50.5	d,L
NMV P44018	_	13.8	23.1		_	_		54.01	
NMV P48392		12.2	21.0			_	—		d,R
NMV P150015	-	16.7	23.6	_				_	d,R
NMV P157343	_	13.0	19.3	>39.0		_	>32.4	—	L
NMV P157344		14.2	19.6						c
OM F1143 (in part)		15.4	25.7					56.1	L
SAM P13118	_	12.6			_				d,R
SAM P17816	_	16.0	23.4					53.5	d,L
			23.9	49.0 (est.)	_			56.3	L
SAM P18693	—	16.7						39.0	d,R
UCMP 53835	_	13.9	18.7*		_				
UCMP 56313	_	13.5*	_						d,R
WAM Unreg. 190	—	_	_	33.8	_		_	_	(juv
WAM 68.5.34	>330	16.6	18.2				-	_	I
D. 'gracilipes'		10.9	21.5				_	_	d,I
QM F1142	_	10.9	21.3						(juv
Metapteryx bifrons	2							34.1	d,1
QM F1135	_	_	~	_	_	_		34.1	(juv
D. ocypus	330			47.1	21.2	20.9	35.5+	53.0	F
SAM P13444	220		_	947 - L	41.4	20.7	al al 4 al	0000	*
D. gidju SAM P26779	_	_		35.0	18.9	14.8+	26.9*	_	p,I
D, sp. AM 'A'	_	10.3	17.1	-		—			(
				15.5					(juv
AM F10850				46.4				_	p,I
NMV P35578		16.2	28.0		_		_	_	d,F
Aves, indet.		21.2	28.0					63.7	d,I
SAM P11552	_	21.2	20.0					05.7	u,1

TABLE 10. Measurements (in mm) of tarsometatarsi of fossil emus (Dromaiinae) from Australia.

	Width, T2	Width, T3	Width, T4	Depth, T2	Depth, T3	Depth, T4
D. novaehollandiae						
AM F771	9.1	23.8	12,2	12.1	20.3	13.9
AM F18935		24.1	12.3		24.1	14.2
QM F1135	5.9	15.7	7.5	8.8	13.8	9.4
QM F1143 (in part)	10.9	27.2	14.3	15.3	25.0	15.8
QM F1143 (in part)	_	23.0			22.6	
NMV L5	>10.5	24.8+	13.2+	>14.0	25.2+	15.9
NMV P44012	> 9.2	24.3	12.8 +	13.1+	22.3+	16.0
NMV P44013	9.8+	24,3	14.5+	15.1	23.8	16.8
NMV P44014	10.9	26.4	13.2	14.8	22.5	15.7
NMV P44015		_			21.4 *	
NMV P44016	10.3	25.9	13.3	13.8	21.4	14.7
NMV P44017	> 8.8	>23.3	>13.1	14.8	23.3	15.4
NMV P44018	> 9.0	25.0+	14.8	13.4+	20.4 +	14.7
NMV P48392	_		>10.5		>21.5	12.4
NMV P150014	11.3	28.3		15.0+	24.0	1.441.7
NMV P150015	14.9+	25.1		11.6	29.8	_
SAM P13118			11.9		20.2+	12.7
SAM P17816	10.0	27.8	>13.3	15.0	23.1	15.6
SAM P18693	12.6	29.8	15.6	>15.3	25.6	>18.0
UCMP 53835		>18.4				- 10.0
UCMP 56313	10.7	27.9		15.3	23.1	
D, 'gracilipes'						
QM F1142		16.6	_		16.5	
		10.0			10.5	_
<i>D. ocypus</i> SAM P13444	10.6	22.0	10.0			
	10.0	27.8	13.5	14.7	21.9	15.7
D. sp.						
AM 'A'	_	16.5		<u> </u>	~14.7	_
QM QA205	—	~16.1			>14.4	_
QM QA416	13.3*			23.9*		_
QM QA505	8.5	17.5		11.9	16.8	_
UCMP RAS5397						
(in part)		15.7+	_	_	14.0+	_
Aves indet.						
SAM P11552	_	>26.3	>14.5		>27.5	_

TABLE 11. Measurements (in mm) of the distal ends of tarsometatarsi of fossil emus (Dromaiinae) from Australia.

\* perhaps T4

SPECIMEN	Phalanx	Length	Proximal Depth	Proximal Width	Element
D. novaehollandiae					
SAM P18059	P1,DII	45.0	20.0	14.8	L
SAM P18248	P2,DII	37.6	17.8	23.8	R
SAM P18249	PI,DIV	38.2	17.6	18.8	R
UCMP 53832	P4,DII or DIV	20.6	10.6	10.5	
UCMP 53832	P1,DII	_	16.7	13.4	р
UCMP 53832	P2,DIV	16.3	12.3	14.1	Ĺ
UCMP 53833	P1,DIV	34.2	16.1	17.8	L
UCMP 53833	P5,DIV?	20.0+	9.6	8.6+	
UCMP 55983	P1,DIII	53.2	20.8	25.7	L
UCMP 55983	P2,DIII	36.2	13.9	21.3	L
UCMP 56849	P1,DII	43.0	18.9	17.0	L
UCMP 94679	P1,DIII	48.4	18.9	24.0	
UCMP 94680	P2,DIII	37.0	18.8	21.4	L
D. gidju					
SAM P26779	P1,DII	33.1	14.2	12.9	L
SAM P26779	P2,DH	23.5	11.8	11.6	L
SAM P26779	P3,DII	19.3	10.1	8.9	L
SAM P26779	P1,DIII	45.1	16.7	19.5	L
SAM P26779	P2,DIII	31.7	12.9	15.2	L
SAM P26779	P3,DIII	22.5	10.5	13.0	L
SAM P26779	P4,DIII	18.4	9.8	10.5	L
SAM P26779	P1,DIV	29.2	13.0	14.0	L
SAM P26779	P2,DIV	16.1	10.6	10.8	L
SAM P26779	P3,DIV	10.8	9.2	9,4	L
SAM P26779	P4,DIV	8.8	7.9	8.2	L
SAM P26779	P5,DIV	15.6	8.8	7.7	L
<i>D</i> . sp.					
QM QA504	P1,DIII	41.5	15.3	16.8	R
UCMP RAS 5397	P2,DII	19.8	11.9	10.9	L

TABLE 12. Measurements (in mm) of phalanges of fossil emus (Dromiinae) from Australia.

TABLE 13. Measurements (in mm) of the fibula of fossil emus (Dromaiinae) from Australia.

SPECIMEN	Proximal Width	Proximal Depth	Element
NMV P157363	17.0	36.4	p,L

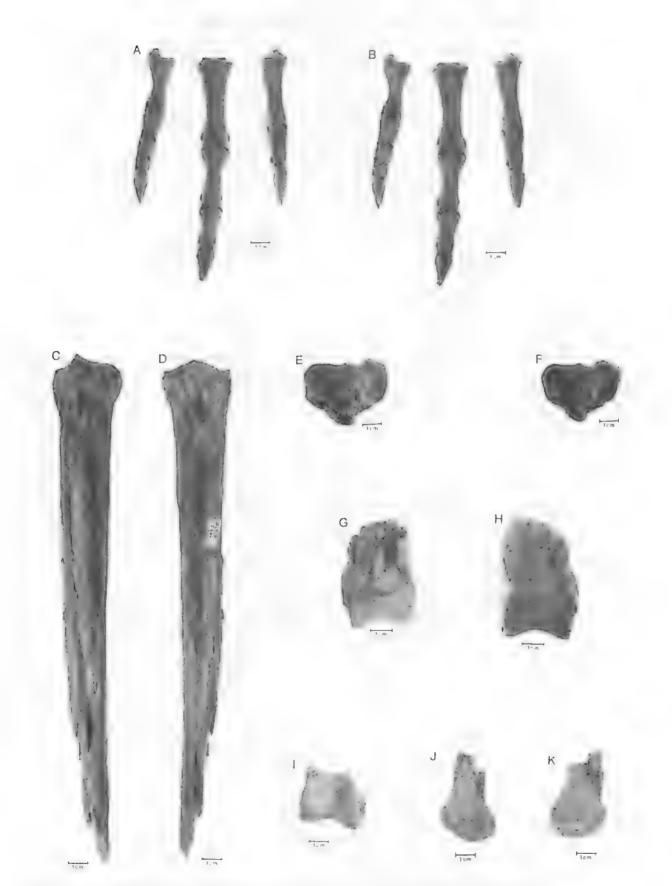


FIGURE 1, Dromaius gidju, n. sp. Type from the Wipajiri Fm. Leaf Locality, Lake Ngapakaldi, Kutjamarpu fauna, Miocene. A,B, stereo pair of pes, dorsal view. C,D,E,F, tarsometatarsi in posterior (C), anterior (D) and proximal (E,F, stereo pair) views. G,H,I,J,K, distal left tibiotarsus in anterior (G), posterior (H), distal (I), internal (J), and external (K) views. Scale indicates 1 cm.



FIGURE 2. Mid-Cainozoic emu fossils from northern South Australia and living casuariids. A-D, posterior views of tarsometatarsi of (A,B) the extant Dromaius novaehollandiae, (C) D. ocypus (SAM P13444), and (D) the extant Casuarius unappendiculatus (from Miller, 1963). E.F. stereo pair in anterior view, tarsometatarsus, the type specimen of *Dromaius ocypus*, SAM P13444, Pliocene, Lawson-Daily Quarry, Mampuwordu Sands, Lake Palankarinna, Palankarinna fauna. G, distal tibiotarsus in anterior view of D. cf. ocypus, RAS 5182, Pliocene. H,I, femur of D. cf. ocypus, in posterior (H) and anterior (I) views, RAS 5176, Pliocene.

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FIGURE 3. A variety of late Cainozoic emu fossils. A, sternum of *Dromaius* sp. in dorsal view, AM F25218. B, pelvic fragment of *D. novaehollandiae* in lateral view, SAM P16501. C, distal left femur in posterior view of *D. novaehollandiae*, HM B801/B934. D,E, proximal right tibiotarsus in lateral (D) and proximal (E) views. F, left tibiotarsus in anterior view, SIAM 61.

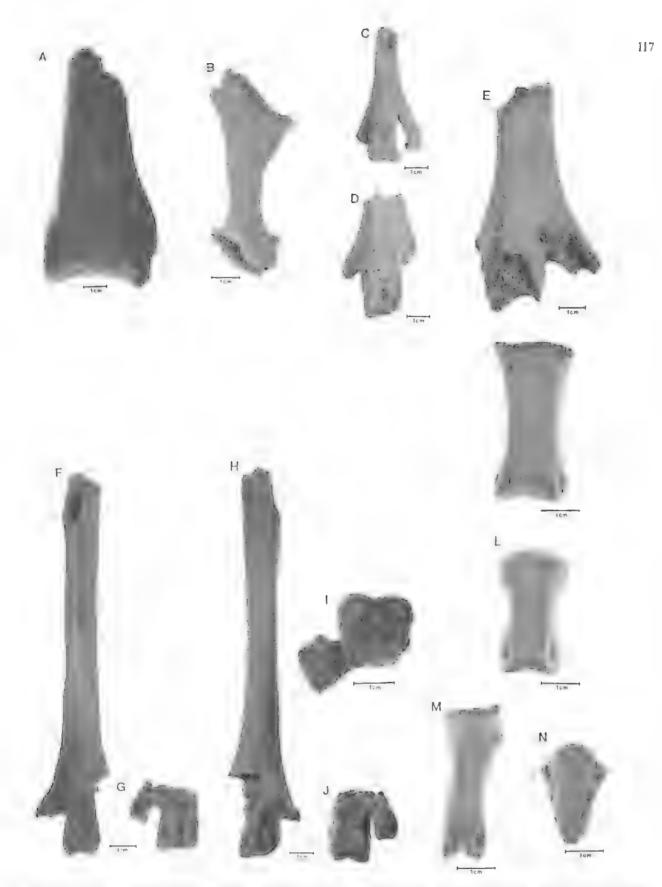


FIGURE 4. A variety of late Cainozoic emu fossils. A, distal right tibiotarsus in anterior view, one of the original type specimens of *Dromaius 'patricus'* De Vis, QM F5548. B, QM F1120 considered by CW. De Vis to be a coracoid of *D. patricus*, but non-avian. C, distal left tarsometatarsus of '*Metapteryx bifrons*' De Vis in anterior view, QM F1135, originally designated a kiwi but actually a juvenile *D. novaehollandiae*. D, distal tarsometatarsus of *D. gracilipes*' De Vis in anterior view, QM F1142, a juvenile *D. novaehollandiae*. E, distal left tarsometatarsus of Aves indet. *cf.* dromornithid in anterior view, SAM P11552, assigned previously as emu. F,H, tarsometatarsus fragment of a small *D. novaehollandiae* in anterior (F) and posterior (H) views, AM 'A', no locality or age data available. G,I,J, second and third trochleae of a small *Dromaius* in posterior (G), distal (I), and posterior (J) views, QW QA505, K-N, phalanges of *D. novaehollandiae* in dorsal views. (K) phalanx 1 digit 111, UCMP 94679; (L) phalanx 2, digit 111, UCMP 94680; (M) phalanx 1, digit 11, UCMP 56849; and (N) ungual phalanx 4, digit 111, UCMP 60563.